

The ecology of freshwater communities of stock water races on the Canterbury Plains

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Abstract

Agricultural intensification on the Canterbury Plains in New Zealand has led to the degradation of natural streams and rivers through lowering of water quality and significant reduction of surface flows from the use of ground and surface water resources. However, this same agricultural expansion has led to the development of a network of permanently flowing open water races to supply stock water to farms across the Canterbury Plains. Stock water races form an extensive network, with approximately 6,500 km of races. Initially I surveyed 62 water races and compared habitat characteristics, water quality, benthic invertebrate and fish communities with nearby natural streams. Races are characterised physically by straight, narrow and shallow channels, and small, uniform substrate. Water races are more turbid than natural streams, and can have high summer temperatures. The benthic macroinvertebrate communities of water races contained a range of taxa, including some not found in natural streams, but communities were less diverse than communities in natural streams, and tended to be dominated by a limited set of generalist taxa. A longitudinal study of three water races showed gradients in physical characteristics of races, including a downstream decrease in channel width, water depth, current velocity and substrate size. However, few strong longitudinal changes to community structure were found, as the generalist taxa commonly occurring in water races were able to tolerate conditions throughout the race network. To test if macroinvertebrate communities were limited by the homogeneous habitat of water races, I conducted a substrate manipulation experiment, where large cobbles and small boulders were added to reaches in five water races. Despite an increase in substrate and current heterogeneity, there were few significant changes to the macroinvertebrate communities over the four months of the manipulation. This outcome does not eliminate low habitat heterogeneity as a limiting factor for water race communities. Rather, the benthic invertebrate community throughout the water race network is a product of the homogeneous habitat, which limits the availability of colonists of taxa that would benefit from increased habitat diversity. A survey of the fish assemblages of water races found races had a depauperate fish community. Only two species were commonly found in water races, and the average species richness of races was 1.5. By contrast natural streams had a higher diversity of fish species (mean

three species), and contained representatives of a greater number of species that are typical of streams and rivers on the Canterbury Plains. My research has shown that stock water races provide an important source of aquatic biodiversity on the plains, both in addition to natural streams and in their own right. However, the biodiversity value of stock water races could be improved with enhancement of in-stream habitat.

1

Introduction

The Canterbury Plains are a lowland area that dominate the central east coast of the South Island of New Zealand, and are the largest flat area in the country, being approximately 180 km long by 70 km wide (Fitzharris et al., 1992). Before the arrival of humans, the plains were covered by podocarp forest and kanuka and manuka scrub (*Leptospermum ericoides* and *L. scoparium*) (McGlone, 1989). The lower plains along the coast were dominated by wetlands and spring systems (Cockayne, 1927), the remnants of which still exist today. Polynesian settlement of New Zealand, approximately 1000 years ago lead to the burning of much of the forest on the Canterbury Plains (Davidson, 1987), and the colonisation by European settlers in the 1840s lead to further vegetation clearance, extensive draining of the wetlands and the development of the land for farming (Wood & Brooking, 2001). Sheep farming and mixed cropping have been the principal agricultural activities in the region since European settlement (Wood & Brooking, 2001), but recent market shifts have lead to a marked increase in intensive dairy farming (Smith & Montgomery, 2004; ABARE & MAF, 2006). This agricultural intensification has negatively affected many of the natural streams and rivers on the plains. Lowered water quality and reduced species diversity are common (Wright-Stow, 2001; Meredith & Hayward, 2002; Meredith et al., 2003; Rickard, 2005), and many streams and small rivers have reduced surface flow (e.g., Larned et al., 2008), which is at least partly caused by the extensive water abstraction that takes place to support the agricultural activities (Taylor & Smith, 1997; Morgan et al., 2002).

Water availability has always been a limiting factor for farmers on the Canterbury Plains, where annual rainfall is low (approximately 625 mm/year; Fitzharris et al., 1992), and summers are frequently hot and dry (de Lisle, 1969). To improve water supply and increase agricultural production, European settlers in the 1880s constructed a network of open waterways to transport water across the plains for stock and domestic purposes (Logan, 1987). Stock water race channels are straight, narrow

and shallow, and provide a homogeneous habitat that contrasts to that of natural streams. However, unlike many natural streams, water races also provide a stable habitat, because they have permanent flow and are buffered from flood events. With approximately 6,500 km of races, the stock water race network is probably the most extensive permanently flowing lotic system on the Canterbury Plains.

There are two other types of manmade channelised waterways on the Canterbury Plains: irrigation races and drains. Canals and races from several extensive surface water irrigation schemes occur alongside much of the stock water race system. During the summer months, these schemes obtain water from Canterbury's large rivers and the Rangitata Diversion Race for border dike and spray irrigation. Most irrigation races do not flow during winter, therefore these systems do not provide a similar habitat to stock water races. Open drains have been built in coastal areas to drain the surrounding farmland where groundwater levels can be high. Water is usually present in drains, though is often slow moving or stagnant. Some stock water races end in drains but are otherwise a distinct system. This thesis focused solely on the stock water race system, although a few water races are jointly used for stock and irrigation water.

Macroinvertebrates are commonly used throughout New Zealand and worldwide to assess the health of streams and rivers (Boothroyd & Stark, 2000). Macroinvertebrates are useful because the structure of their communities changes along environmental gradients (Quinn & Hickey, 1990b; Harding & Winterbourn, 1995; Harding et al., 1999). Therefore where strong gradients may occur, such as along systems subject to increasing agricultural intensity, macroinvertebrates may provide useful indicators of changing conditions. Macroinvertebrates also have advantages over traditional water chemistry measurements, which are often measured at just one moment in time, as they provide a more integrated assessment of overall environmental quality (Boothroyd & Stark, 2000). Macroinvertebrates are used by most of the regional councils in New Zealand, including the Canterbury Regional Council (Environment Canterbury), which uses macroinvertebrates for State of the Environment monitoring and its stream biomonitoring program. The macroinvertebrate communities of streams and rivers on the Canterbury Plains have also been studied by researchers documenting the impacts of floods, drying and agricultural activities on freshwater

systems (Sagar, 1986; Scrimgeour et al., 1988; Wright-Stow, 2001; Rickard, 2005; Datry et al., 2007). However, despite the abundance of stock water races in Canterbury, their ecology has received little attention. The research described in this thesis fills this gap in knowledge, and examines the value of stock water races as an aquatic habitat on the Canterbury Plains, and as a refuge for taxa threatened by habitat loss in natural streams.

This thesis is presented as four stand-alone research manuscripts. For this reason, there is some repetition of introductions and methods. The first data chapter (chapter 2) describes the physical and chemical habitat features of the stock water race channels. It also compares the benthic macroinvertebrate communities in the water races to those in natural streams to assess the importance of water races as a habitat for macroinvertebrate biodiversity on the Canterbury Plains, and as a refuge for taxa affected by habitat loss in natural streams. Chapter three is an investigation of longitudinal gradients in physical and chemical characteristics and macroinvertebrate and fish communities in three water races. A substrate addition experiment is described in chapter four, which tested if the benthic macroinvertebrate communities of water races were limited by the heterogeneous physical conditions of the water race habitat. The fifth chapter characterises the fish communities of stock water races and compares them to those of natural streams to determine whether water races provide a refuge for fish species and a habitat for fish biodiversity on the Canterbury Plains. Finally, I conclude the thesis with a brief summary which reviews the key findings from this thesis and suggest possible management actions that could improve the biodiversity value of stock water races.

2

A comparison of habitat characteristics and benthic invertebrate communities of stock water races and natural streams on the Canterbury Plains, New Zealand

Abstract

Long-term agricultural development has resulted in major modifications to flow regimes in river systems globally. The Canterbury Plains of New Zealand are home to intensive agricultural activities, and many 2nd–4th order streams in the region are now seasonally ephemeral or have intermittent surface flows along their length. However, this same agricultural expansion has fostered the development of an extensive artificial, but permanently flowing, stock water race system. The stock water races form a network of waterways that traverse the Canterbury Plains. This study compared the benthic macroinvertebrate communities in 62 stock water races and 20 natural stream sites in order to determine the distinctiveness of the water race communities and their value as refugia for benthic species present in ephemeral natural streams. A total of 58 taxa were collected, 10 were unique to water races and 9 unique to natural streams. Water race communities had lower diversity than natural streams, and were dominated by a common, limited ‘set’ of generalist taxa, including *Potamopyrgus* (Prosobranchia: Hydrobiidae), *Deleatidium* (Ephemeroptera: Leptophlebiidae) and *Hydora* (Coleoptera: Elmidae), that were able to tolerate the conditions throughout the race network. In contrast, the natural streams, with a greater variability of habitats and less degraded abiotic conditions, supported a greater variety of community assemblages. In central areas of the Canterbury Plains water races frequently provide the only connected, permanent surface water habitat for benthic macroinvertebrate species. These systems are refugia for a number of stream taxa that are able to tolerate the highly modified habitat available in water races.

Introduction

For the last 150 years, the Canterbury Plains has been one of the most intensively farmed regions of New Zealand (Wood & Brooking, 2001). Canterbury is a water deficit region, with low annual rainfall of approximately 625 mm/year (Fitzharris et al., 1992), and summers that are frequently hot and dry (de Lisle, 1969). In the 1880s, European settlers sought to improve water supply and increase agricultural production on the plains by diverting water from streams and larger braided rivers into several purpose-built open race networks (Logan, 1987). The primary purpose was to supply stock and domestic drinking water to farms across the region. Although many farms now source water from aquifers for stock, irrigation and domestic purposes, the complex network of water races remain, and are still used by many farmers. Currently, there are approximately 6,500 km of stock water races traversing the plains, making them an extensive network of permanently flowing surface water in the region.

The stock water races on the Canterbury Plains are entirely modified ecosystems. Compared to natural streams, they are highly physically modified, with narrow, straight, shallow channels, regulated discharge and homogeneous substrate. These characteristics create a hydrologically stable and largely unvaried habitat. In contrast, the region's natural streams are influenced by unpredictable floods and summer drying (Sagar, 1986; Scrimgeour et al., 1988; Datry et al., 2007; Larned et al., 2008), have natural riffle-pool complexes and heterogeneous substrates. These natural systems can be divided into two broad groups: large, permanently flowing braided rivers (Gage, 1969; Gray et al., 2006), and smaller 3-4 order rivers, which typically exhibit permanent flow in the foothills and lower reaches near the coast, but have subsurface flow in their mid-reaches during summer (Datry et al., 2007; Larned et al., 2008). Water abstraction for intensive agriculture is one of the major causes of reductions in surface flow of small rivers and streams on the plains (Taylor & Smith, 1997; Morgan et al., 2002).

Benthic macroinvertebrate communities in streams are strongly influenced by flow regimes, especially extreme conditions such as floods and droughts (Lake 2000).

Because so many streams and small rivers on the Canterbury Plains are now seasonally ephemeral or have significant drying reaches, the benthic fauna have become disjunct and patchy in distribution. For example, in the Selwyn River, which flows from the foothills to the sea, the mid-reaches have surface flow for only 30 days per annum. Consequently, the benthic diversity is high in the headwaters and lower reaches, but depleted in the mid-reaches where surface flow is ephemeral (Datry et al., 2007).

By contrast, the stock water races have permanent flow throughout the year. With no flood or drying disturbance, they provide a hydrologically stable habitat for benthic macroinvertebrates, and in mid summer provide almost all of the surface flow habitat across much of the plains. Consequently, the stock water race network may provide an important refuge for the Canterbury Plains's stream species. However, much of the Canterbury Plains are subjected to intensive agricultural activities. The negative consequences of agriculture on streams and rivers, including alteration of physical habitat, reduced water quality and modification of biotic communities are well documented (Quinn & Hickey, 1990a; Quinn & Hickey, 1990b; Quinn et al., 1992; Scott et al., 1994; Harding & Winterbourn, 1995; Matson et al., 1997, Pimentel et al., 1997; Delong & Brusven, 1998; Wright-Stow, 2001; Rickard, 2005). As the stock water system is located in the heart of a region dominated by intensive agriculture, I expect the physical, chemical and biological characteristics of the stock water races system to be strongly influenced by agricultural activities.

In this study I characterised the habitat of Canterbury stock water races and compared benthic macroinvertebrate communities in the races with communities in neighbouring small natural streams and rivers in order determine the distinctiveness of the water race communities and their value as refugia for benthic species threatened by drying in nearby natural streams.

Methods

Study system

The Canterbury Plains dominate the central east coast of the South Island of New Zealand, and comprise the largest flat area in the country, being approximately 180 km long by 70 km wide (Fitzharris et al., 1992). The plains are bounded by the foothills of the Southern Alps to the west, and the Pacific Ocean to the east. Historically, cash cropping and sheep farming have been the principal agricultural activities in the region, but market shifts have led to a marked increase in intensive dairy farming (Smith & Montgomery, 2004; ABARE & MAF, 2006).

The water race network is maintained by four local government authorities: the Waimakariri, Selwyn, Ashburton and Timaru District Councils. Water for the system is sourced from a number of different rivers, streams and springs on the plains (Table 1). Each water race system includes several large feeder races, which carry water from intakes at local rivers. Smaller lateral races branch off the feeder races, which then often branch to smaller races. Smaller races frequently rejoin to larger races, creating a complex network. The water races flow for roughly 65 km across the plains from the foothills to the coast, ending in sinkholes and drains, with relatively few discharging directly into the ocean.

Table 1. Rivers that supply water to the stock water race networks in each of the four local council districts on the Canterbury Plains.

District	Source river(s)
Waimakariri	Waimakariri River
Selwyn	Waimakariri, Kowhai, Selwyn, Hororata, Rakaia rivers
Ashburton	Rakaia, North Ashburton, South Ashburton, Rangitata River, plus numerous small streams and springs
Timaru	Orari River

In this study, a total of 62 sites in water races were selected from surveyor's and GIS maps (Fig. 1). Sites were divided between the four district water race systems, with the number of sites in each district corresponding roughly to the size of the system. A range of water race sizes were sampled, from large feeder races near the foothills to smaller races near the coast. Difficulties accessing races on private property meant

that most sites were located where races crossed or ran alongside public roads. Twenty sites in natural streams were also sampled. These streams and small rivers were all in the vicinity of the stock water race systems, however included a wide range of stream types, including streams near the foothills, small ephemeral rivers, coastal springs and spring tributaries of large braided rivers.

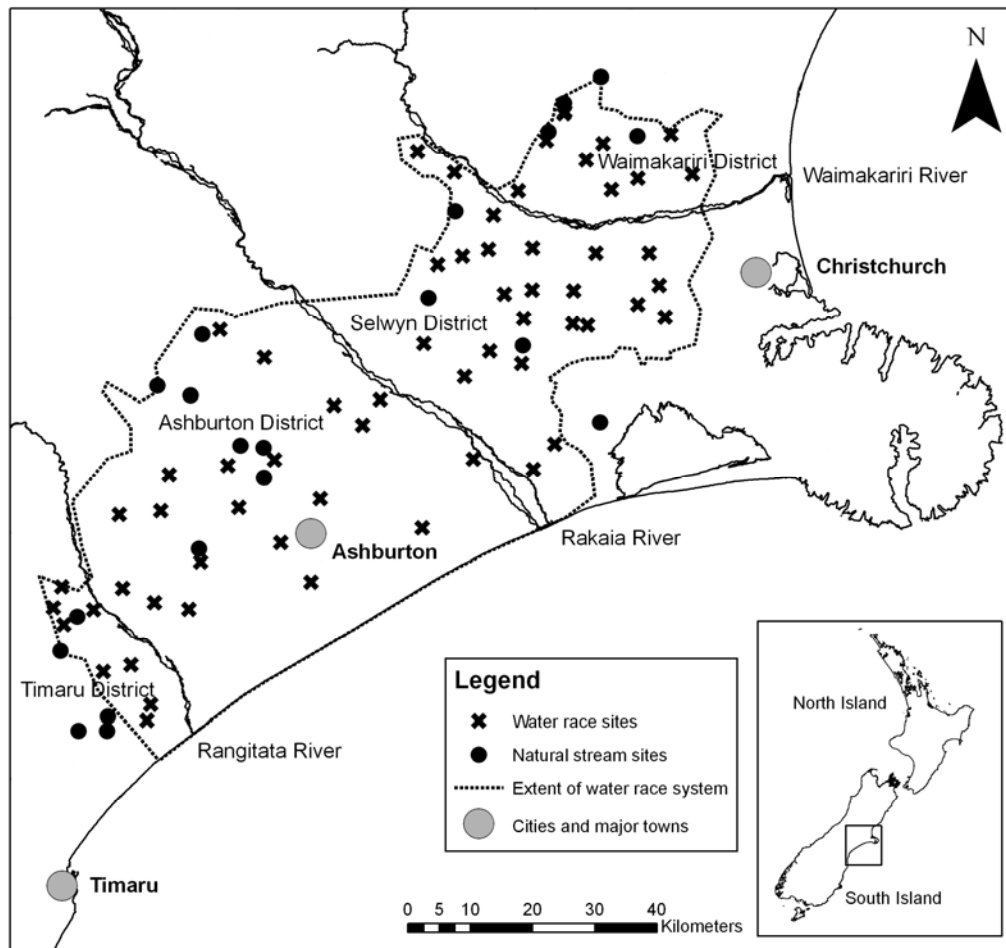


Figure 1. Map showing the 62 water race sites and 20 natural stream sites sampled on the Canterbury Plains.

Sample collection and processing

All sites were sampled on a single occasion during the austral summer in December 2006 – January 2007 or in January 2008. A range of physical, chemical and biological parameters were collected at each site. Each site consisted of a reach of approximately 10 m and as pools are essentially absent in stock water races, all sites selected were in riffle-run complexes. At each site, mean current velocity and depth were determined at three different points across a transect (Marsh-McBirney flow mate 2000), and channel width at water level was measured. Mean substrate size and substrate heterogeneity was estimated by measuring the longest axis of 30 randomly selected particles. Substrate was characterised using the Wentworth scale (Cummins, 1962). Bank and channel stability was assessed using the subjective channel evaluation method described by Pfankuch (1975), where a reach score of <38 is excellent; 39-76, good; 77-114, fair, and >115, poor. Spot measurements of water temperature and chemical parameters, including conductivity and dissolved oxygen (DO), were taken in the field using standard meters (Oakton pH/CON10 and YSI 550A). Turbidity (NTU) was measured in the laboratory using a portable Hach turbidimeter 2100P.

Both qualitative and quantitative benthic macroinvertebrate samples were collected. In order to collect as many taxa as possible an extensive kick-net (250 μm mesh) sample was collected, while quantitative data was assessed by collecting three replicate Surber samples (0.09 cm^2 , 500 μm mesh) at random locations in stony riffles or runs. Samples were preserved in 90% ethanol in the field, sieved in the laboratory with a 500 μm sieve, and sorted and identified to the lowest taxonomic group possible in the laboratory using the keys of Winterbourn (1973) and Winterbourn et al. (2006).

Quantities of the three important energy sources for aquatic macroinvertebrates, coarse particulate organic matter (CPOM > 1 mm; Cummins, 1974), suspended organic seston and benthic algae, were determined. CPOM was extracted from the three Surber samples during laboratory processing and suspended organic seston was estimated from three replicated 50 μm mesh plankton net samples. Benthic algal biomass was determined from 8 cm^2 scrapings from 5 randomly collected stones. The CPOM, seston and algae samples were oven dried at 35°C, weighed, and then ashed at 550°C to determine organic ash free dry weight (AFDW) (Steinman et al., 2007).

Data analysis

Data for all physical, chemical and biotic characteristics of water races and natural streams was compared using two sample t-tests. Data was log or square root transformed if it was not normally distributed, and Mann-Whitney U tests were used for data that could not be transformed satisfactorily. Significant differences for all analyses were accepted at $P < 0.05$.

Substrate heterogeneity was estimated using the standard error of the mean of the 30 particles. Three biotic indices were generated in order to compare natural stream and water race communities: the Macroinvertebrate Community Index (MCI, Stark 1985), which is based on presence-absence data, its semi-quantitative version (SQMCI, Stark 1998) and its quantitative version (QMCI, Stark 1993). The indices are based on the tolerances of macroinvertebrates in stony riffles to organic enrichment (Stark, 1985) and allow classification of sites into degradation categories (Stark 1998): MCI > 120 (QMCI/SQMCI > 6) indicates clean water; 100–120 (5–6), doubtful quality or possible pollution; 80–100 (4–5), probable moderate pollution; < 80 (< 4), probable severe pollution. Community evenness was calculated using the Berger-Parker index, which expresses the proportional importance of the most dominant species (May 1975). The number of sensitive taxa (Ephemeroptera, Plecoptera and Trichoptera [EPT]) was calculated, as was the percentage of the community occupied by EPT taxa and tolerant taxa (Mollusca, Chironomidae [Diptera] and Oligochaeta). To compare taxonomic richness in an equal number of water race sites to natural stream sites, S_{obs} (Mao Tau) rarefaction of water race data was calculated using EstimateS (Colwell, 2006). S_{obs} (Mao Tau) rarefaction is sample-based and estimates species richness for a subsample of the pooled total species richness, based on the number of species actually discovered (Gotelli & Colwell, 2001). Canonical correlation analysis (CCA) was used to assess the distributions of taxa occurrence amongst sites, and their associations with the physicochemical variables using PC-ORD (McCune & Mefford, 1999).

Results

Physical and chemical characteristics

The stock water races were significantly narrower and shallower than the natural streams, although current velocity did not differ significantly from natural streams (Table 2). Water races were generally dominated by small substrate, particularly pebbles. While a few water races had small cobbles, boulders were rare. Fine sediment was relatively common in races (mean 12% of substrate, $SE \pm 0.6\%$, range 0–90%). Benthic substrate of natural stream was significantly larger, dominated by cobbles (Table 2), and fine sediment was uncommon (mean 0.5%, $SE \pm 1.5\%$, range 0–3%; significantly lower than in water races, $P < 0.0001$). Substrate heterogeneity was significantly lower in the water races than the natural streams (Table 2). The index of channel stability (Pfankuch, 1975) rated most water races as ‘good’ and a few as ‘fair’, and was significantly lower than natural streams, which were all rated as ‘good’ except one (Table 2). Eight of the 20 natural stream sites (40%) dried at some stage during summer, most of these for at least one month, while no water races dried during the study.

Table 2. Physical, chemical and primary energy source values for water races and natural streams (water races $n = 62$, natural streams $n = 20$). Statistics are t -test or Mann-Whitney U test, $P < 0.05$. Significance codes: n.s. non significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Water race		Natural stream		<i>t</i> -stat	<i>P</i>
	Mean (1SE)	Range	Mean (1SE)	Range		
<i>Physical</i>						
Channel width (m)	1.0 (0.04)	0.5 – 2.2	6.2 (1.3)	1.6 – 25	9.109	***
Depth (m)	0.15 (0.09)	0.05 – 0.38	0.19 (0.16)	0.09 – 0.41	2.173	*
Current velocity (ms ⁻¹)	0.45 (0.03)	0.12 – 1.09	0.56 (0.07)	0.16 – 1.32	1.659	n.s.
Substrate size (cm)	2.7 (0.1)	0.3 – 5.8	6.3 (0.6)	2.0 – 12.1	6.111	***
Substrate heterogeneity (SE of mean)	0.40	0.2 – 1.0	0.65	0.2 – 1.4	4.385	***
Channel stability (Pfankuch)	65 (1)	45 – 95	57 (2)	42 – 77	3.040	***
Temperature (°C)	18.5 (0.5)	11.6 – 26.7	17.1 (0.6)	13.3 – 22.6	1.502	n.s.
<i>Chemical</i>						
Conductivity (μS @ 25°C)	65 (4)	12 – 217	99 (13)	58 – 317	3.808	***
DO (mg/L)	10.0 (0.1)	6.7 – 12	10.0 (0.3)	6.8 – 12.8	0.007	n.s.
Turbidity (NTU)	11 (1)	0.9 – 38.8	3 (1)	0.4 – 23	6.216	***
<i>Primary energy sources</i>						
CPOM (g m ² AFDW)	22.4 (5.4)	1.4 – 317	9.9 (2.6)	1.3 – 42	3.139	**
Suspended organic seston (g m ³ AFDW)	0.07 (0.1)	0 – 0.67	0.05 (0.02)	0 – 0.29	2.424	*
Benthic algal biomass (g m ² AFDW)	6.14 (0.9)	0 – 36.6	3.4 (0.7)	0 – 12.5	2.015	*

Nearly one third of the water races had spot temperatures over 20°C, compared to 10% of natural streams, however the average water race temperature was not significantly higher than that of natural streams (Table 2). Generally, water races increased in temperature downstream, probably due to a combination of limited shading and a decreasing volume of water to buffer sunshine (temperature correlated with distance from source river $r^2 = 0.11$, $P = 0.0045$). Conductivity was significantly lower in the water races, whereas DO levels were generally high and very similar between water races and natural streams. Water races were significantly more turbid than natural streams (Table 2). AFDW of CPOM was 200% greater in water races than in natural streams. AFDW of suspended seston and benthic algal biomass were also significantly greater in water races than in natural streams (Table 2).

Benthic macroinvertebrates

A total of 58 benthic macroinvertebrate taxa were collected from the water races and natural streams. Of these, 49 taxa were identified in the 62 water races and 48 taxa in the 20 natural streams. Water races and natural streams shared 39 taxa, with 10 taxa found in races but not streams, and 9 taxa found in streams but not races. When taxonomic richness was rarefied to account for the lower number of natural stream sites, water race richness decreased to 37 taxa for 20 sites, which was markedly lower than the 48 taxa recorded for the 20 natural stream sites. However, mean taxonomic richness did not differ significantly between water races and natural streams (Fig. 2). Similarly, invertebrate density and the Berger-Parker evenness index were not significantly different in water races and natural streams (Fig. 2).

The Macroinvertebrate Community Index (MCI) and its variants (QMCI and SQMCI) gave variable results, although the mean values for all three differed significantly between water races and natural streams (Fig. 3). Natural streams had higher index values than the water races for all indices, and were categorized in the higher end of the ‘probable moderate degradation’ category for the MCI and the ‘possible mild degradation’ for the QMCI and SQMCI. On average, water races were in the ‘probable moderate degradation’ category for all indices (Stark 1998) (Fig. 3). The QMCI and SQMCI both classified water races evenly across all 4 categories, however MCI classified almost all races in the 2 lowest categories. The QMCI and SQMCI placed 60% of the natural streams in the highest category (‘clean water’), with the

remainder spread across the other 3 categories. However, the MCI classed very few natural streams in the highest category.

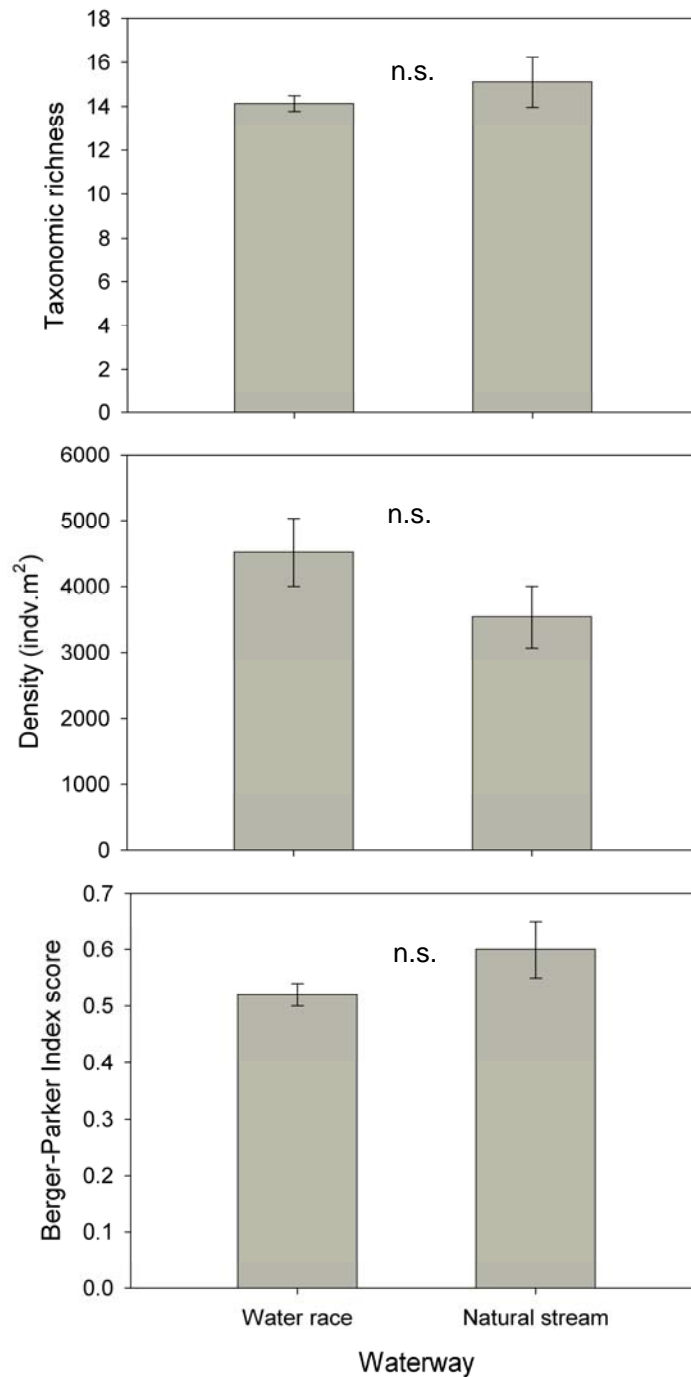


Figure 2. Comparison of water race and natural stream benthic macroinvertebrate taxonomic richness, density (individuals per m²) and community evenness (Berger-Parker Index) (mean \pm 1SE; water races n = 62, natural streams n = 20). Statistics are *t*-test, $P < 0.05$. Significance codes: n.s. non significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

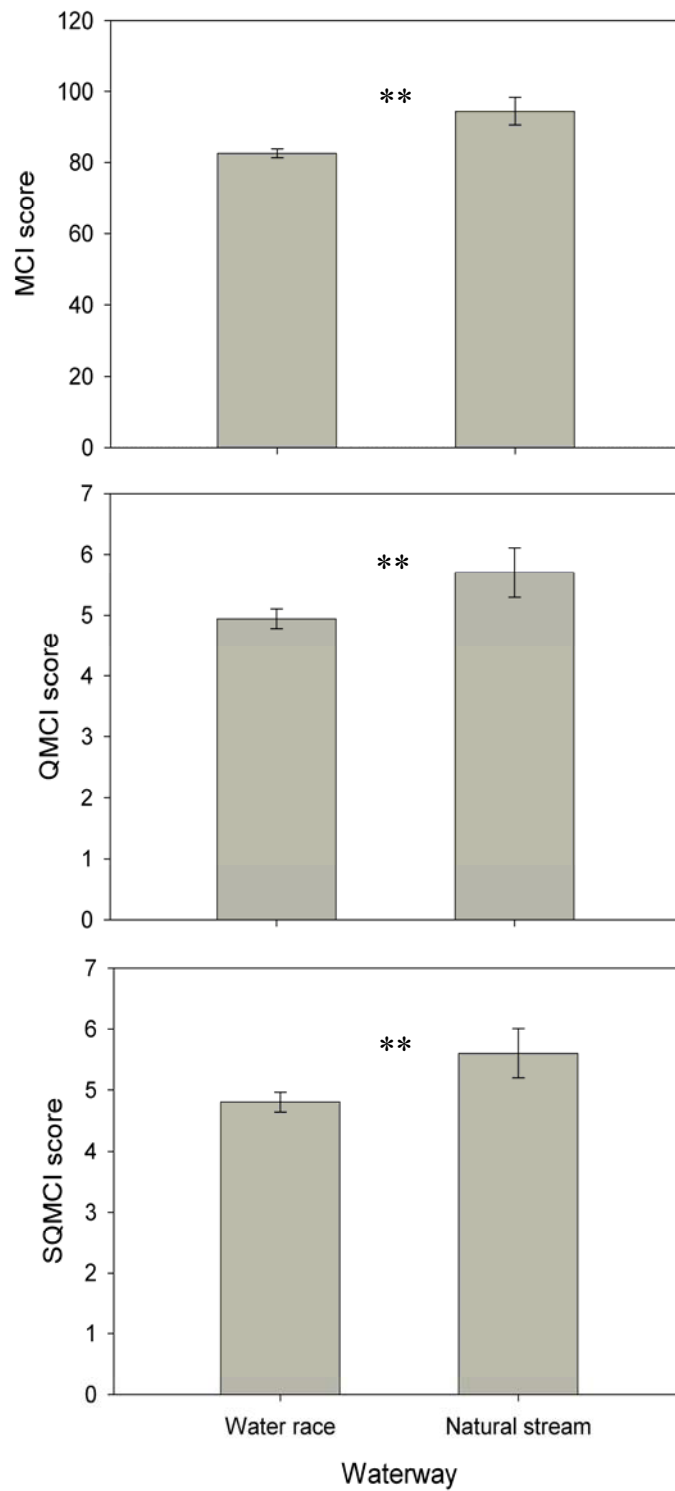


Figure 3. Comparison of biotic indices of water races and natural streams for MCI, QMCI and SQMCI (mean \pm 1SE; water races $n = 62$, natural streams $n = 20$). Statistics are t -test or Mann-Whitney U test, $P < 0.05$. Significance codes: n.s. non significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The number and percentage of EPT taxa were significantly higher in natural streams (Fig. 4), while water race communities had significantly higher percentage of molluscs than natural streams (Fig. 5). By contrast, there was no significant difference between the percentage of chironomids in water races and natural stream communities, with this family accounting for only 5% and 10% of the benthic communities, respectively. Oligochaetes were also uncommon, accounting for a very small percentage of water race and natural stream communities, but constituted a significantly higher proportion in the races (Fig. 5).

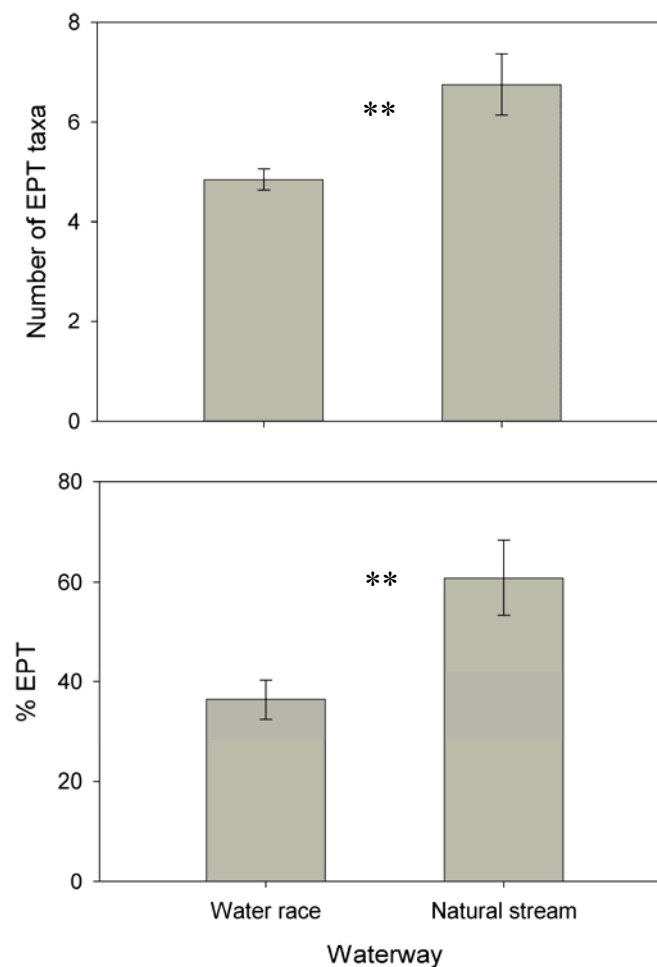


Figure 4. Comparison of number of EPT taxa and % EPT in water races and natural streams (Mean \pm 1SE; water races $n = 62$, natural streams $n = 20$). Statistics are t -test or Mann-Whitney U test, $P < 0.05$. Significance codes: n.s. non significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

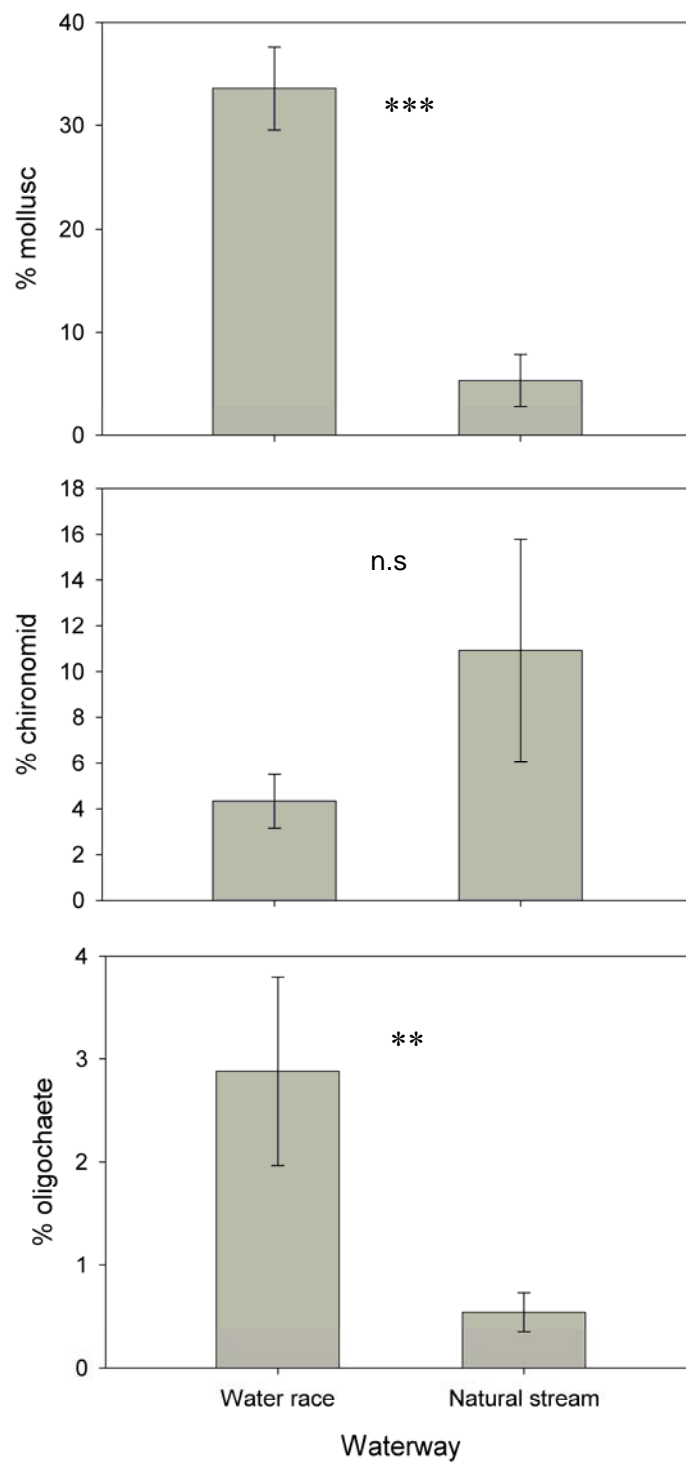


Figure 5. Comparison of % mollusc, % chironomid and % oligochaete in water races and natural streams (Mean \pm 1SE; water races $n = 62$, natural streams $n = 20$). Statistics are t -test or Mann-Whitney U test, $P < 0.05$. Significance codes: n.s. non significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

An ordination based on presence-absence data showed that occurrence of benthic macroinvertebrate taxa was reasonably similar among water races, indicating that most water races shared a common set of taxa (Fig. 6). In comparison, there was high variability in benthic macroinvertebrate communities among the natural streams. The ordination also indicated several environmental factors that may be influencing the communities. Natural streams communities appeared to differ from the water races primarily due to differences in channel width, substrate size and substrate heterogeneity (Fig. 6). Among the water races, the ordinations suggested a current velocity–temperature gradient influenced macroinvertebrate communities (Fig. 6).

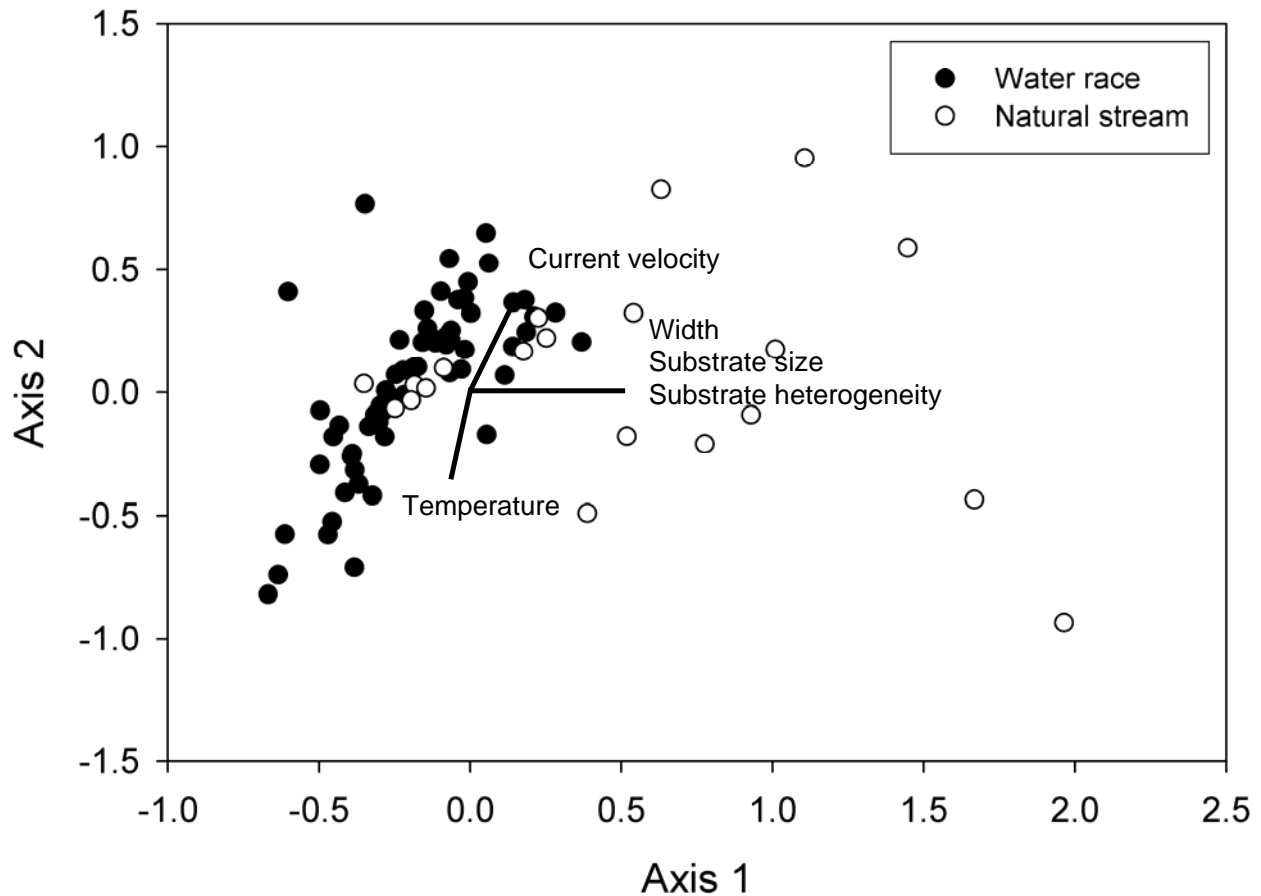


Figure 6. Canonical correlation analysis illustrating the relative occurrence of benthic macroinvertebrate taxa in water races and natural streams and the environmental variables associated with their distribution (water race $n = 62$, natural stream $n = 20$).

The 10 most common taxa varied between water races and natural streams (Table 3). Although they shared 8 of the 10 most common taxa, the order of incidence varied considerably. The elmid beetle *Hydora* was found in almost all water races and the hydrobiid snail *Potamopyrgus* sp. was the second most common benthic macroinvertebrate, found in 95% of the races. *Hydora* was also common in natural streams, but *Potamopyrgus* was far less common. All natural stream sites had the leptophlebiid mayfly *Deleatidium* sp. The two commonest trichopterans in water races were *Hudsonema amabile* (Leptoceridae) and *Pycnocentrodes* sp. (Conesucidae), while in natural streams, two hydrobiosids, *Hydrobiosis* sp. and *Psilochorema* sp., were most common. Orthocladiinae (Diptera: Chironomidae), *Austrosimulium* (Diptera: Simuliidae) and *Physa* (Pulmonata: Physidae) were common in both water races and natural streams (Table 3), while *Aoteapsyche* (Trichoptera: Hydropsychidae) was only common in the natural streams.

Table 3. The ten most frequently occurring benthic macroinvertebrate taxa and the percent of sites in which they were found in water races and natural streams (water race n = 62, natural stream n = 20).

Water race			Natural stream	
Taxa	% of sites		Taxa	% of sites
1	<i>Hydora</i>	98	<i>Deleatidium</i>	100
2	<i>Potamopyrgus</i>	95	<i>Hydrobiosis</i>	90
3	Oligochaeta	87	Orthocladiinae	90
4	<i>Deleatidium</i>	87	<i>Hydora</i>	90
5	Orthocladiinae	85	<i>Psilochorema</i>	85
6	<i>Hudsonema</i>	82	<i>Aoteapsyche</i>	75
7	<i>Pycnocentrodes</i>	76	<i>Austrosimulium</i>	75
8	<i>Austrosimulium</i>	76	Oligochaeta	70
9	<i>Hydrobiosis</i>	74	<i>Pycnocentrodes</i>	65
10	<i>Physa</i>	69	<i>Physa</i>	60

Despite similarities in the taxa found in these systems, the community composition of water races differed from natural streams (Fig. 7). In the water races, molluscs were the most dominant taxa, with *Potamopyrgus* accounting for 85%. Ephemeroptera (99.99% *Deleatidium*), Coleoptera (99.8% *Hydora*) and Trichoptera made up most of the remainder of the water race communities (Fig. 7). In natural stream communities Ephemeroptera comprised almost 50% of communities, with 99.4% being *Deleatidium* (Fig. 7). Trichoptera, Coleoptera (99.8% *Hydora*), Chironomidae and other Diptera (76% *Austrosimulium*) formed most of the remainder.

Two notable macroinvertebrates found in the water races in the Ashburton district were freshwater crayfish (*Paranephrops zealandicus*) and freshwater mussels (*Hyridella* sp.), the latter having a conservation listing of gradual decline (Hitchmough et al., 2007). Both occurred in a range of size classes, indicating that populations can survive in water races, although freshwater mussels were uncommon. Freshwater mussels were not found in the natural streams in this study.

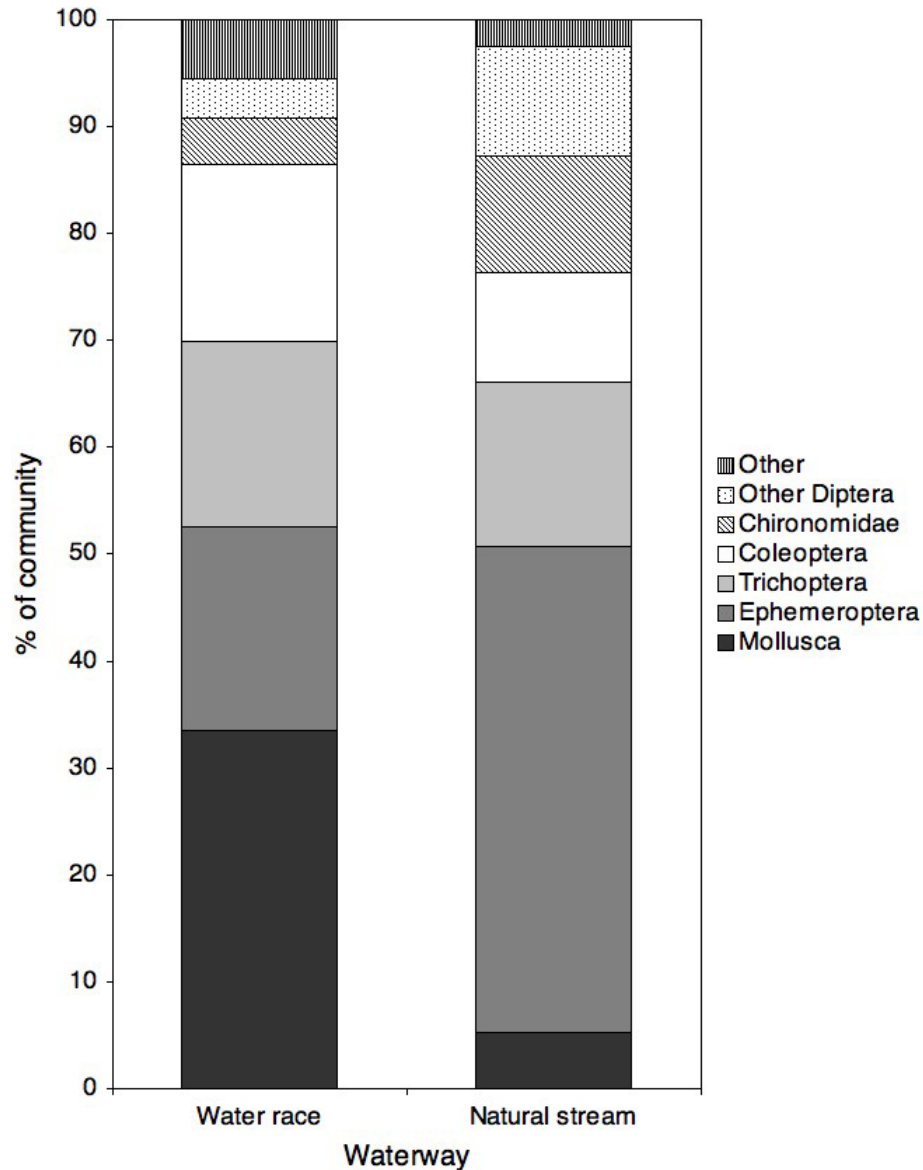


Figure 6. The mean community composition of benthic macroinvertebrates in water races and natural streams (water race n = 62, natural stream n = 20).

Discussion

The stock water race system on the Canterbury Plains is an extensive network, covering areas where surface water can be scarce in summer (Datry et al., 2007; Larned et al., 2008). Furthermore, their flow regimes are relatively stable, as they are buffered from floods and drying. Thus, these race networks provide an important permanent lotic habitat on the Canterbury Plains. However, the water races are a highly modified system, characterised by uniform, narrow channels and low discharge. Water races had no pools, only riffles and runs, and substrate was pebble dominated and relatively homogeneous. These physical features of water races contrasted with the natural streams in this study, which had heterogeneous channel beds, riffle-run-pool complexes, and a diversity of substrate sizes.

The differences in physical habitat between the water races and natural streams are likely to influence the composition of their benthic macroinvertebrate communities. For example, the greater substrate size and heterogeneity in natural streams increased the diversity of habitats, and consequently should have promoted greater invertebrate taxonomic richness in those systems (Hynes, 1970; Allan, 1975; Minshall, 1984; Douglas & Lake, 1994; Beisel et al., 1998; Boyero, 2003). In addition, larger and more heterogeneous substrates cause an increase in small-scale current heterogeneity, which may also have increased habitat diversity in the natural streams (Allan & Castillo, 2007).

Water races were also likely to be strongly influenced by the intensive agricultural activities present on the Canterbury Plains. Numerous studies have documented the effects of agriculture on Canterbury streams (Harding & Winterbourn, 1995; Wright-Stow, 2001; Meredith & Hayward, 2002; Meredith et al., 2003; Rickard, 2005), and although many of the natural streams in this study would have been similarly affected, the size and location of the water races makes them likely to be heavily impacted by agricultural activities. Agricultural activities often alter important aspects of stream habitat that influence invertebrate communities (Quinn, 2000). Absent or modified riparian vegetation, which is common to streams in agricultural areas (Williamson et al., 1992; Delong & Brusven, 1994; Davies-Colley, 1997; Riley et al., 2003), can lead

to elevated water temperature (Quinn et al., 1992; Harding & Winterbourn, 1995) and increases in turbidity and sedimentation from increased catchment and stream bank erosion (Williamson et al., 1992; Quinn & Stroud, 2002; Riley et al., 2003). Removal or modification of riparian vegetation can also reduce habitat availability for terrestrial adult aquatic insects (Collier & Smith, 1997). In this study, I found one third of water races, but only two natural streams, had spot temperatures over 20°C. Temperatures over this level can restrict the occurrence of some macroinvertebrate taxa, for example, stoneflies and mayflies are generally scarce in rivers where the maximum temperature exceeds 19 and 21.5°C respectively (Quinn & Hickey, 1990a). Also, turbidity (in my study systems this was probably primarily suspended sediment) and deposited sediment were both higher in the water races. This could have negatively affected the benthic macroinvertebrates in the water races through mechanisms including abrasion, infilling of hyporheic habitat and reduction of food quality (Graham, 1990; Ryan 1991; Quinn, 2000). Although turbidity may have been partially caused by turbidity in the source river, annual cleaning by diggers, raw or lightly vegetated channel banks and stock trampling probably also increases turbidity levels in races (Williamson et al., 1992; Riley et al., 2003).

Despite the homogeneous and sometimes degraded habitats of the water races, a range of benthic macroinvertebrate taxa were found in riffles and runs in these systems. However, the most common taxa in water races tended to be those with broad habitat requirements that are reasonably tolerant of organic enrichment, sedimentation and higher temperatures (Winterbourn, 1981; Stark, 1985; Quinn et al., 1994). The mean taxonomic richness of the water races was similar to that of the natural streams, however rarefaction of water race data indicated that races probably had a lower richness than natural streams. The richness of both water races and natural streams in this study was generally lower than other streams and small rivers in Canterbury, especially compared to those outside of the intensively farmed plains (Harding, 1994; Harding & Winterbourn, 1995; Wright-Stow, 2001; Rickard, 2005).

Stream health indices indicated water races were generally in poorer condition than natural streams, although results among the indices were variable. The MCI indicated that almost all the water races were 'probably severely' or 'moderately' degraded (Stark, 1998). However, the QMCI and SQMCI allocated water races reasonably

evenly through all 4 categories, suggesting around half of races have 'healthier' communities dominated by more sensitive taxa. Because presence-absence data is used to calculate the MCI, it takes no account of the relative abundance of the taxa (Stark 1985, 1993), and consequently reflects taxonomic rather than numerical composition (Stark 1998). Therefore, the MCI reflected the greater number of more tolerant taxa in water races, and the QMCI and SQMCI indicated that these tolerant taxa do not always dominate the water race communities.

The differences in ecosystem health scores were driven by fundamental differences in the benthic community structure of the water races and natural streams. EPT taxa, which are generally sensitive to modifications of stream environments, comprised a significantly lower proportion of the community in the water races than in natural streams. Sensitive taxa are often absent or less abundant in streams modified by agricultural activities (Quinn & Hickey, 1990b; Quinn et al., 1992; Harding & Winterbourn, 1995; Quinn et al., 1997; Harding et al., 1999), as they are less tolerant of stressors such as high temperatures, pollution and sedimentation, (Scott, 1973; Winterbourn, 1981; Stark, 1985; Ryan, 1991; Quinn et al., 1994). Conversely, taxa tolerant of modified stream environments, such as molluscs, oligochaetes, and chironomids, tend to dominate communities in streams that are impacted by agricultural activities (Quinn & Hickey, 1990b; Quinn et al., 1992; Harding & Winterbourn, 1995; Quinn et al., 1997; Harding et al., 1999), and the two former taxa were more abundant in the water races than the natural streams.

Conclusion

Stock water races contained a range of benthic macroinvertebrate taxa, despite being highly physically modified, having homogeneous habitat, and being subject to the impacts of agricultural activities. The compositions of benthic macroinvertebrate communities in the water races were distinct to natural streams. The natural streams, with their greater variability of habitats, supported a variety of benthic macroinvertebrate community assemblages. In comparison, the benthic invertebrate communities throughout the water race system were dominated by a common set of

generalist taxa, predominantly *Deleatidium*, *Potamopyrgus* and *Hydora*, which were able to tolerate the conditions in most water races.

Although the water races supported a lower number of macroinvertebrate taxa to natural streams, many natural stream taxa also occurred in water races. The water races could therefore provide alternative habitat for some stream species during dry periods in natural streams. Flying adult insects from nearby races could be a potential source of colonists for natural streams when flow returns. However, a number of taxa that were common in natural streams were not present in water races, consequently races do not provide refuge for all freshwater macroinvertebrate taxa found on the Canterbury Plains.

There has been ongoing debate about closing stock water races (e.g., RF, 2006), for various reasons, including easing pressure on source rivers, freeing up allocation for other users, inefficiency, and poor water quality (Morgan et al., 2002). However this study suggests that the water races support a diverse benthic fauna, contain a number of taxa that may not also be present in natural streams and provide a potential source of colonists for ephemeral streams across the plains. Furthermore, a number of water races contain 'healthier' communities that are comparable to natural streams in the area. The stock water race system therefore provides an important freshwater ecosystem and a habitat for aquatic macroinvertebrate biodiversity on the Canterbury Plains, although this is limited by the highly modified form of the water race channels.

3

Gradients in physical and chemical parameters and biotic communities along artificial waterways in an agricultural landscape

Abstract

Longitudinally, natural streams and rivers are broadly predictable in their hydrological and morphological characteristics. In general, natural systems increase in flow volume and have predictable zones of transition in physical flow characteristics from the headwaters to the lower reaches. In some biomes, streams also undergo a change in primary food source, as the influence of detritus from riparian vegetation decreases, and algal resources and fine detritus increases. Benthic macroinvertebrate community structure exhibits a corresponding adjustment to these longitudinal gradients. In anthropogenic landscapes these characteristic gradients may be markedly altered. I investigated longitudinal patterns in physical and chemical characteristics, energy sources, and biotic communities in three artificial waterways that represent extreme anthropogenic modification of the natural stream condition. Stock water races are small, managed, permanent waterways that are used to provide drinking water for livestock across the Canterbury Plains in New Zealand. The water races are narrow channels with low discharge, a homogeneous flow and small, uniform substrate. Unlike natural streams, the branching structure of the water race network resulted in a downstream reduction in channel width, water depth, current velocity and substrate size. Water temperature increased longitudinally, but changes in water chemistry were minor. As low-biomass exotic grasses dominated the riparian vegetation, autochthonous primary production was the primary energy source along the length of the water races. The benthic macroinvertebrate and fish communities of the water races were dominated by a limited set of mostly generalist taxa. Although the density and relative abundance of common benthic macroinvertebrate taxa changed longitudinally, because most taxa were tolerant of the degraded conditions in the races there was no strong longitudinal community change downstream.

Introduction

Understanding and defining predictable longitudinal gradients in river systems has been fundamental to many of the advances in stream ecology theory. In particular, the River Continuum Concept (RCC) proposed by Vannote et al. (1980) has played a major role in focussing research into stream ecosystem theory. The RCC uses physical gradients to explain longitudinal patterns in ecosystem-level processes and benthic communities within river systems. The concept was proposed as a framework for river systems worldwide, but its applicability has since been the subject of intense discussion, with many caveats and modifications proposed (Winterbourn et al., 1981, Barmuta & Lake, 1982; Winterbourn, 1982; Minshall et al., 1983; Cowie, 1985; Statzner & Higler, 1985; Ryder & Scott, 1988; Thomson & Townsend, 2000). An alternative, but not necessarily conflicting, hypothesis was proposed by Statzner and Higler (1986), who suggested that physical characteristics of flow (termed 'stream hydraulics'), such as streambed hydraulic stress, create transition zones that influence the general pattern of stream invertebrate communities.

Although these models are influenced by global patterns in biomes and regional biogeography that alter the patterns in community structure (Minshall et al., 1983; Cushing et al., 1983), many of their concepts can be applied to most natural stream systems (Cushing et al., 1995). As natural streams flow from their headwaters to lowland rivers, they undergo a series of predictable changes in physical attributes and primary energy sources (Vannote et al., 1980; Statzner & Higler, 1986). Stream morphology, including width, current velocity, flow volume and substrate size change downstream to create a gradient of physical conditions (Nevins, 1965; Statzner & Higler, 1986; Statzner et al., 1988; Church, 2002). In their RCC, Vannote et al. (1980) describe a change from predominantly terrestrial energy inputs (from riparian vegetation) in small headwater streams, to mostly autochthonous primary production and organic matter that has been transported from upstream in the larger downstream reaches. Benthic macroinvertebrate community structure often exhibits a corresponding adjustment to these longitudinal gradients, as shown by studies of a variety of biomes (Hawkins & Sedell, 1981; Canton & Chadwick, 1983; Cushing et

al., 1983; Grubaugh et al., 1996; Usseglio-Polatera & Beisel, 2002; Greathouse & Pringle, 2006).

Freshwater systems worldwide are subject to increasing levels of anthropogenic modification, particularly from impoundments, urbanisation and agriculture (Allan & Flecker, 1993; Matson et al., 1997; Pimentel et al., 1997). As the influence of these human impacts on river systems intensifies, research into models of river systems are required to incorporate the effects of anthropogenic impacts on longitudinal gradients. Studies of the effects of impoundments have revealed discontinuities in macroinvertebrate communities (Voelz & Ward, 1990; Harding, 1992; Ogbeibu & Oribhabor, 2002; Young et al., 2004; Armitage, 2006), and urbanisation and agriculture have been shown to cause an overall decline in species diversity and domination of communities by pollution tolerant species (Quinn & Hickey, 1990b; Quin et al., 1992; Scott et al., 1994; Harding & Winterbourn, 1995; Delong & Brusven, 1998; Wright-Stow, 2001; Rickard, 2005; Walsh et al., 2007).

This study investigates the stock water race system on the Canterbury Plains. Stock water races are an extreme example of anthropogenic modification to waterways. They were built in the 1880s by European farmers to improve water supply and increase agricultural production (Logan, 1987). The water races transport water from local rivers through a complex network of small, highly modified channels to farms across the Canterbury Plains. The branching structure of the water race system results in a progressive size decrease size with increasing distance from the race source. This might be expected to cause longitudinal gradients in a number of abiotic features in water races, and should result in a corresponding adjustment in biotic community structure. Because the water races flow through an intensive agricultural landscape, physical, chemical and biotic features of water races may also be affected by agricultural activities, as are many natural streams on the plains (Wright-Stow, 2001; Meredith & Hayward, 2002; Meredith et al., 2003; Rickard, 2005).

I investigated longitudinal gradients in the physical, chemical and biological characteristics of stock water races to determine whether morphological gradients in a highly modified waterway system create predictable, corresponding changes to benthic macroinvertebrate and fish community structure.

Methods

Study system

The Canterbury Plains dominate the central east coast of the South Island of New Zealand, and comprise the largest flat area in the country, being approximately 180 km long by 70 km wide (Fitzharris et al., 1992). The plains are bounded by the foothills of the Southern Alps to the west, and the Pacific Ocean to the east. Historically, cash cropping and sheep farming have been the principal agricultural activities in the region, but market shifts have led to a marked increase in intensive dairy farming (Smith & Montgomery, 2004; ABARE & MAF, 2006).

Natural river systems on the Canterbury Plains can be divided into two broad groups: large, permanently flowing, braided rivers (Gage, 1969; Gray et al., 2006), and smaller 3-4 order rivers, which typically exhibit permanent flow in the foothills and lower reaches near the coast, but have subsurface flow in their mid reaches during summer (Datry et al., 2007; Larned et al., 2008). There are approximately 6,500 km of stock water races traversing the plains, and as many of the plain's smaller rivers dry seasonally in their mid-reaches, water races probably provide the most extensive network of permanent flowing surface water in the region.

The water race system is maintained by four local government authorities: the Waimakariri, Selwyn, Ashburton and Timaru District Councils. Water for the system is sourced from a number of different rivers, streams and springs on the plains. Each water race system includes several large feeder races, which carry water from intakes at local rivers. Smaller lateral races branch off the feeder races, which then often branch to smaller races. Smaller races frequently rejoin to larger races, creating a complex network. The water races flow for roughly 65 km across the plains from the foothills to the coast, ending in sinkholes and drains, with relatively few discharging directly into the ocean.

Three stock water races, one in each of the Waimakariri, Selwyn and Ashburton Districts, were sampled at five sites along their length (Fig. 1). The five sites on each race were roughly evenly spaced down the system, with site 1 located in a feeder race

near the source river, and site 5 near the end of the race. Although most water race intakes are at rivers near the foothills, the Selwyn and Ashburton race systems have additional water intakes at several points down the plains. Only water races that began near the foothills were used, to provide the greatest length of waterway possible. The distance of each site down the length of a water race was measured from the race intake at the source river (Table 1).

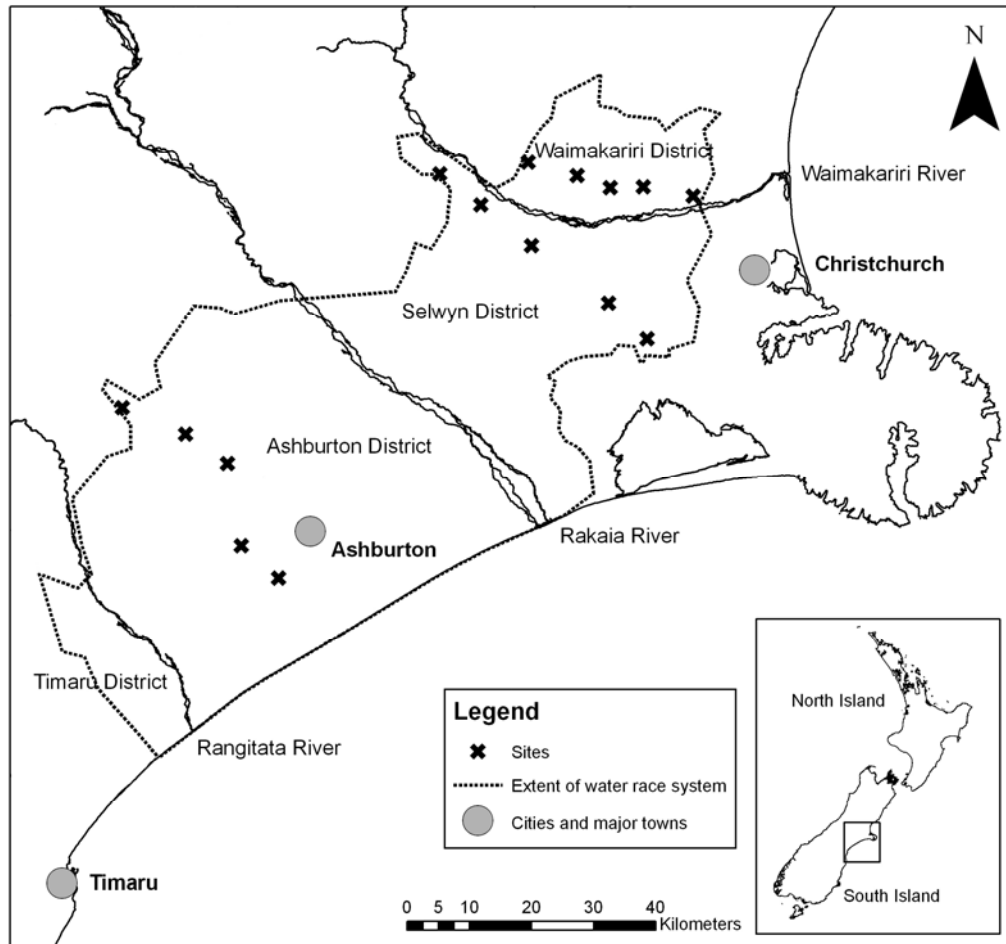


Figure 1. Map showing the 15 water race sites sampled on the Canterbury Plains.

Table 1. Distance of each site downstream from the source river for each of the three water races (one per district).

District	Site	Distance from the source river (km)
Waimakariri	1	12
	2	22
	3	28
	4	33
	5	43
Selwyn	1	18
	2	26
	3	37
	4	52
	5	60
Ashburton	1	6
	2	18
	3	29
	4	44
	5	53

Sample collection and processing

All sites were sampled on a single occasion during the austral summer between December 2006 and February 2007. A range of physical, chemical and biological parameters were collected at each site. Each site consisted of a reach of approximately 10 m and, as pools are essentially absent in stock water races, all sites were in riffle-run complexes. At each site, mean current velocity and depth were determined at three different points across a transect (Marsh-McBirney flow mate 2000), and channel width was measured at water level. Mean substrate size and substrate heterogeneity was estimated by measuring the longest axis of 30 randomly selected particles. Substrate was characterised using the Wentworth scale (Cummins, 1962). Bank and channel stability was assessed using the subjective channel evaluation method described by Pfankuch (1975), where a reach score of <38 is excellent; 39-76, good; 77-114, fair, and >115, poor. Spot measurements of water temperature, conductivity and dissolved oxygen (DO), were taken in the field using standard meters (Oakton pH/CON10 and YSI 550A). Turbidity was measured in the laboratory using a portable Hach turbidimeter (2100P). Total nitrogen and total phosphorus levels were measured from spot samples that were processed by the Environment Canterbury water laboratory using standard methods (SM 4500-N B and SM 4500-P I; APHA, 2005).

Both qualitative and quantitative benthic macroinvertebrate samples were collected. In order to collect as many taxa as possible, an extensive kick-net (250 μm mesh) sample was collected, while quantitative data was assessed by collecting three replicate Surber samples (0.09 cm^2 , 500 μm mesh) at random locations in riffles or runs. Samples were preserved in 90% ethanol in the field, sieved in the laboratory with a 500 μm sieve, and sorted and identified to the lowest taxonomic group possible, using the keys of Winterbourn (1973) and Winterbourn et al. (2006).

Quantities of the three important energy sources for aquatic invertebrates, coarse particulate organic matter (CPOM > 1 mm; Cummins, 1974), suspended organic seston and benthic algae, were determined. CPOM was extracted from the three Surber samples during laboratory processing, and suspended organic seston was estimated from three replicated 50 μm mesh plankton net samples. Algal biomass was determined from 8 cm^2 scrapings from five randomly collected stones. The CPOM, seston and algae samples were oven dried at 35°C, weighed, and then ashed at 550°C to determine organic ash free dry weight (Steinman et al., 2007).

Eleven of the 15 water race sites were electric fished using a Kainga backpack electric fishing machine (EFM300; NIWA Instrument Systems, Christchurch, New Zealand) in a 20 m reach using the 3 pass removal technique. Two sites were too swift for fishing and two did not have a complete 20 m reach accessible. Fish were counted and identified live in the field to species according to McDowall (2000) and released.

Data analysis

A linear model with groups (water race) was used to test for a water race effect for each physical, chemical and biotic variable. Because there was no water race effect, linear regressions were used to investigate relationships between variables and distance from the source river. Data that was not normally distributed was log or square root transformed. Significant relationships were accepted at $P < 0.05$.

Substrate heterogeneity of the 30 particles was estimated using the standard error of the mean. The stream 'health' of the water races was measured by generating three biotic indices from the benthic invertebrate data: the Macroinvertebrate Community

Index (MCI, Stark 1985), which is based on presence-absence data, its semi-quantitative version (SQMCI; Stark, 1998), and its quantitative version (QMCI; Stark, 1993). The indices are based on the tolerances of macroinvertebrates in stony riffles to organic enrichment (Stark, 1985) and allow classification of sites into degradation categories (Stark, 1998): MCI >120 (QMCI/SQMCI >6) indicates clean water; 100–120 (5–6), doubtful quality or possible pollution; 80–100 (4–5), probable moderate pollution; <80 (<4), probable severe pollution. Community evenness of the benthic macroinvertebrate assemblage was calculated using the Berger-Parker index, which expresses the proportional importance of the most dominant species (May, 1975). The number of sensitive taxa (Ephemeroptera, Plecoptera, Trichoptera [EPT]) was calculated, and the percentage of the community occupied by EPT and tolerant taxa (Mollusca, Chironomidae, Oligochaeta). Canonical correlation analysis (CCA) was used to assess the distributions of taxa abundance amongst sites, and their associations with the physicochemical variables using PC-ORD (McCune & Mefford, 1999).

Results

Physical and chemical characteristics

Water race channel width, water depth and current velocity all decreased significantly with distance from the source river (Fig. 2). Water race channel width exhibited the strongest relationship with distance, decreasing from 2–3.5 m at the upstream end of the race to only 0.5–1.0 m in the lower reaches (Fig. 2). Substrate size also decreased significantly downstream, from small cobble-sized particles in the upper reaches, to small pebbles in the lower reaches (Fig. 3). This reduction in substrate size may be partly due to an increased intensity of dredging of water races in lower reaches of the network. Diggers are used annually in many smaller races to remove aquatic and riparian vegetation that obstruct flow, and it is likely larger particles are removed in the process. Substrate heterogeneity decreased longitudinally, linked to the decrease in substrate size (Fig. 3). While the channel stability index of Pfankuch (1975) gave values ranging from 53 to 74 (mean: 60), indicating these races had stable channels, the index did not change significantly longitudinally. Water temperature increased significantly downstream (Fig. 3). Conductivity, turbidity, DO, total phosphorous and total nitrogen did not change significantly downstream (Table 2).

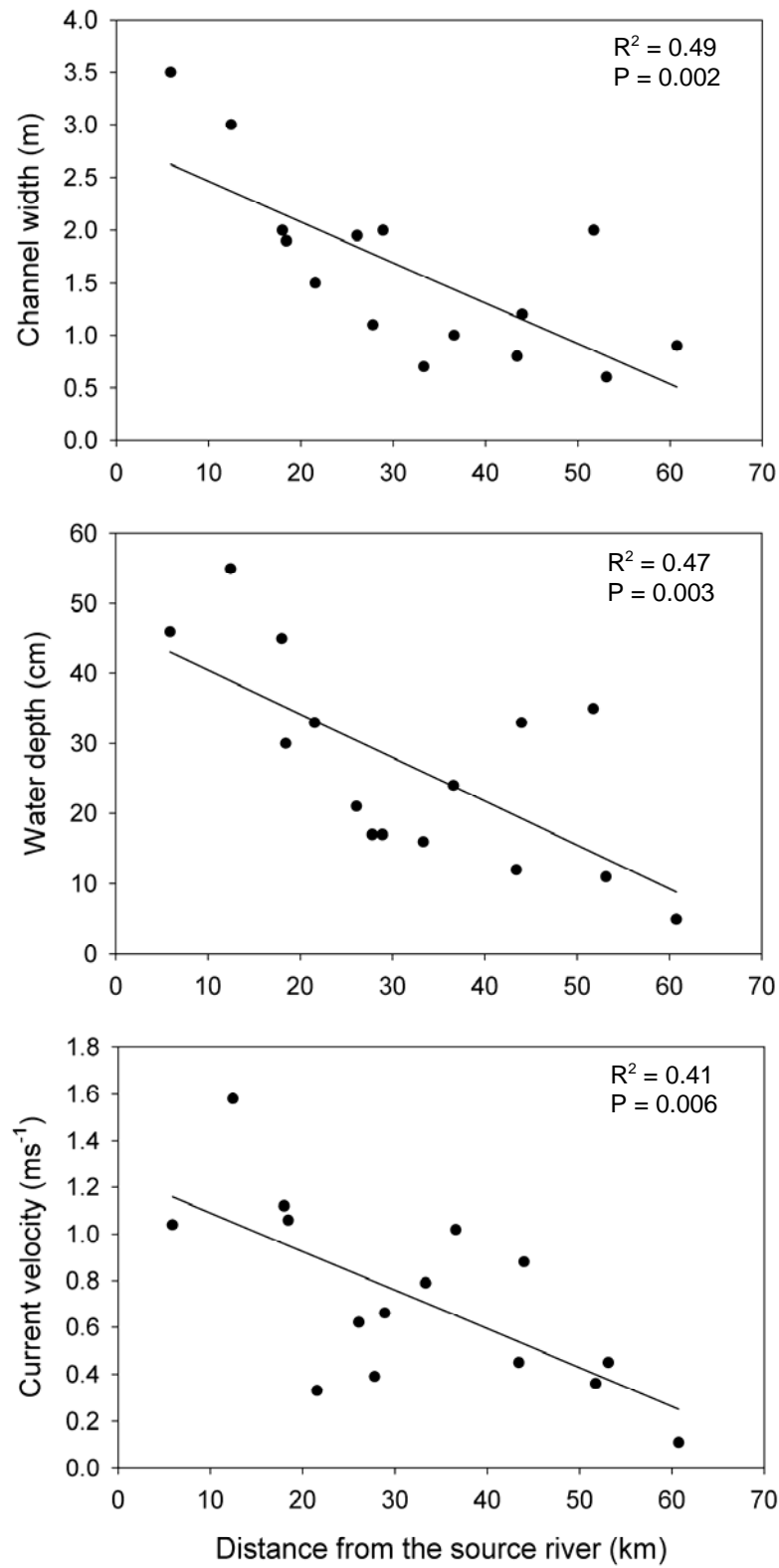


Figure 2. Relationship between distance from the source river and channel width, water depth and current velocity.

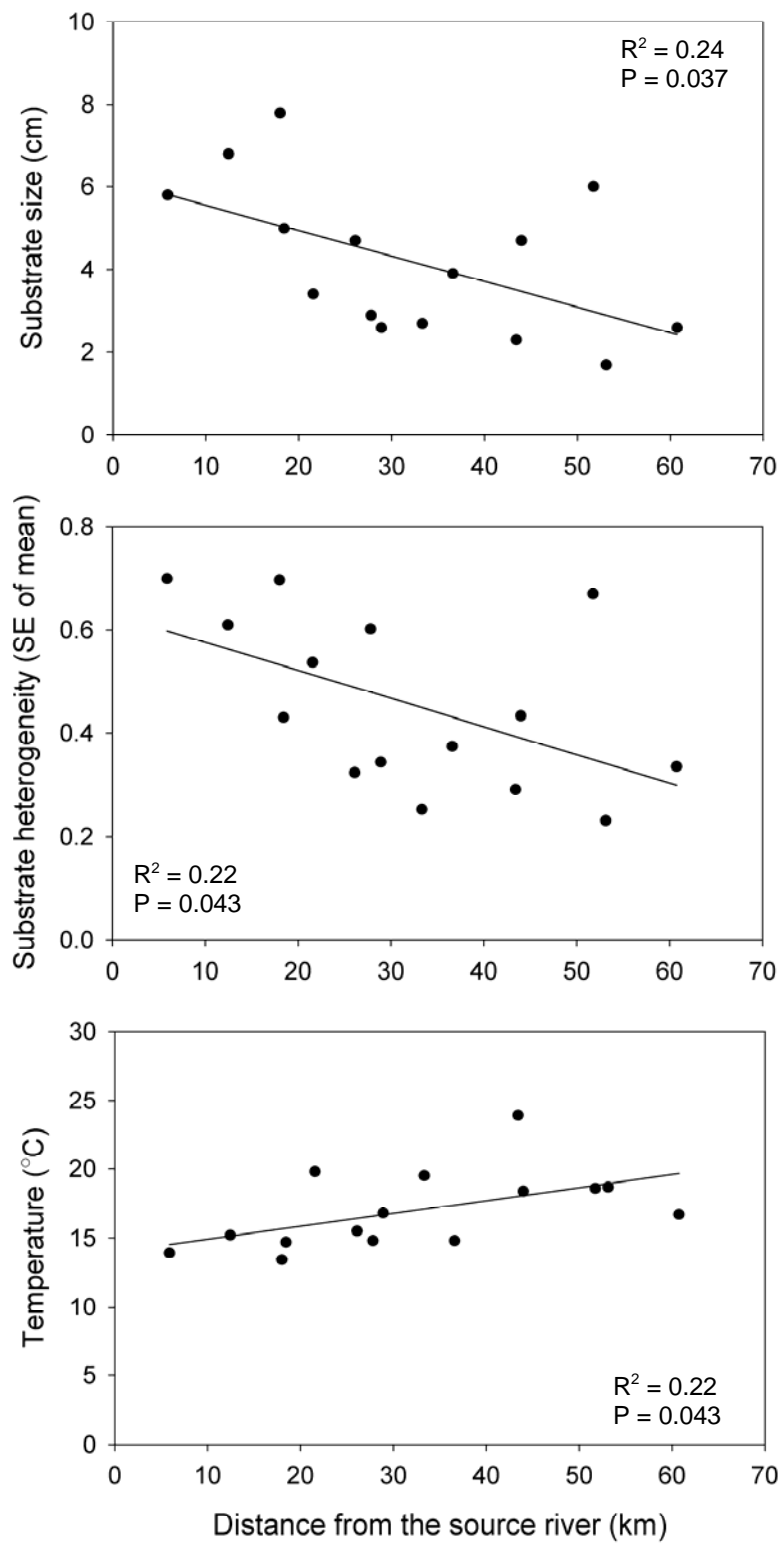


Figure 3. Relationship between distance from the source river and mean substrate size, substrate heterogeneity and water temperature.

Table 2. Mean (1SE) values of the chemical parameters for the five longitudinal sites (the three water races combined).

	1	2	Site 3	4	5
Conductivity ($\mu\text{S @ } 25^\circ\text{C}$)	81 (5)	79 (4)	74 (6)	77 (5)	76(2)
Turbidity (NTU)	6 (1)	11 (3)	9 (2)	13 (2)	10 (4)
DO (mgL)	11.0 (0.2)	10.8 (0.4)	10.4 (0.4)	10.8 (0.7)	9.2 (0.7)
TN (mgL)	0.11 (0.40)	0.05 (0.02)	0.13 (0.05)	0.06 (0.04)	0.19 (0.14)
TP (mgL)	0.013 (0.002)	0.017 (0.004)	0.013 (0.0003)	0.018 (0.004)	0.023 (0.005)

Primary energy source

There was no longitudinal change in suspended organic seston, CPOM or benthic algal biomass (Table 3). This was probably strongly linked to riparian vegetation type (mostly exotic grasses) remaining relatively unchanged down the length of the water races.

Table 3. Mean (1SE) values of the primary energy sources for the five longitudinal sites (the three water races combined).

	1	2	Site 3	4	5
Suspended organic seston (g m^{-3} AFDW)	0.02 (0.02)	0.07 (0.05)	0.09 (0.05)	0.05 (0.01)	0.03 (0.01)
CPOM (g m^{-2} AFDW)	11.6 (3.6)	13.1 (7.0)	20.0 (8.3)	13 (3.0)	23 (10.0)
Benthic algal biomass (g m^{-2} AFDW)	4.4 (3.4)	3.6 (0.7)	24.9 (10.8)	14.8 (12.4)	4.4 (1.7)

Benthic macroinvertebrates

A total of 34 benthic macroinvertebrate taxa were found in the 15 water race sites, with an average taxonomic richness at each site of 14.6 (S.E. +/- 0.75, range 11 – 22). Taxonomic richness did not change longitudinally (Fig. 4). An average of 7.5 taxa (range: 5 – 12) accounted for >1% of the community at each site. The four most common taxa were the mayfly *Deleatidium* sp. (Leptophlebiidae), the caddisfly *Aoteapsyche* sp. (Hydropsychidae), *Potamopyrgus* sp. (Prosobranchia: Hydrobiidae) and *Hydora* (Elmidae) beetles, and together they accounted for 82% (S.E. +/- 2.25, range 61% – 97%) of the community (Fig. 5). *Hydora* and *Potamopyrgus* were present at all sites, and *Deleatidium* and *Aoteapsyche* at all but one. Benthic

macroinvertebrate communities in these water races had very low richness, which would be expected to influence the magnitude of longitudinal community changes.

Despite the presence of common taxa at almost all sites, their abundance and proportion did change longitudinally. *Aoteapsyche* decreased significantly in abundance ($r^2 = 0.37$, $P = 0.01$) and decreased in proportion of the community ($r^2 = 0.25$, $P = 0.03$). *Hydora* increased significantly in abundance ($r^2 = 0.69$, $P = <0.001$) and proportion of the community ($r^2 = 0.45$, $P = 0.004$) (Fig. 5 & 6). The abundance and proportion of the community of *Deleatidium* and *Potamopyrgus* tended to increase down the length of the water races, however this was variable and not significant (Fig. 5 & 6). The significant increase in total invertebrate density downstream (Fig. 4) was a combination of the initial increase in *Deleatidium* abundance, the later increase in molluscs (especially *Potamopyrgus*) and *Hydora*, and also an increase in a number of the less common taxa.

An ordination of relative abundance of taxa highlighted longitudinal differences in community composition (Fig. 7). The most obvious community differences were between the sites at each end of the race network; those up to 20 km from the source river were grouped together and were separated from those more than 30 km from the source river. However, sites 20–30 km from the source river were spread throughout the figure, indicating they had more variable community compositions (Fig. 7).

There was a slight longitudinal decrease in the MCI, and although this was not significant, it did indicate that there was a loss of sensitive taxa and and/or gain of tolerant taxa (i.e., a slight decrease in stream ‘health’) (Fig. 4). There was no change in QMCI, SQMCI, the number of EPT taxa, or the Berger-Parker community evenness index. However, the proportion of sensitive taxa did change longitudinally; percent EPT decreased significantly ($r^2 = 0.25$, $P = 0.03$), changing from approximately 80% of the community within 20 km from the source river to approximately 30% of the community in the lower reaches of the network (Fig. 8). This was predominantly caused by the marked decline in *Aoteapsyche* abundance, and a decrease in *Deleatidium* in the lower reaches. Percent mollusc increased longitudinally, mostly due to an increase in *Potamopyrgus*, however this was not significant (Fig. 8). There was no change in % chironomid or % oligochaete (Fig. 8).

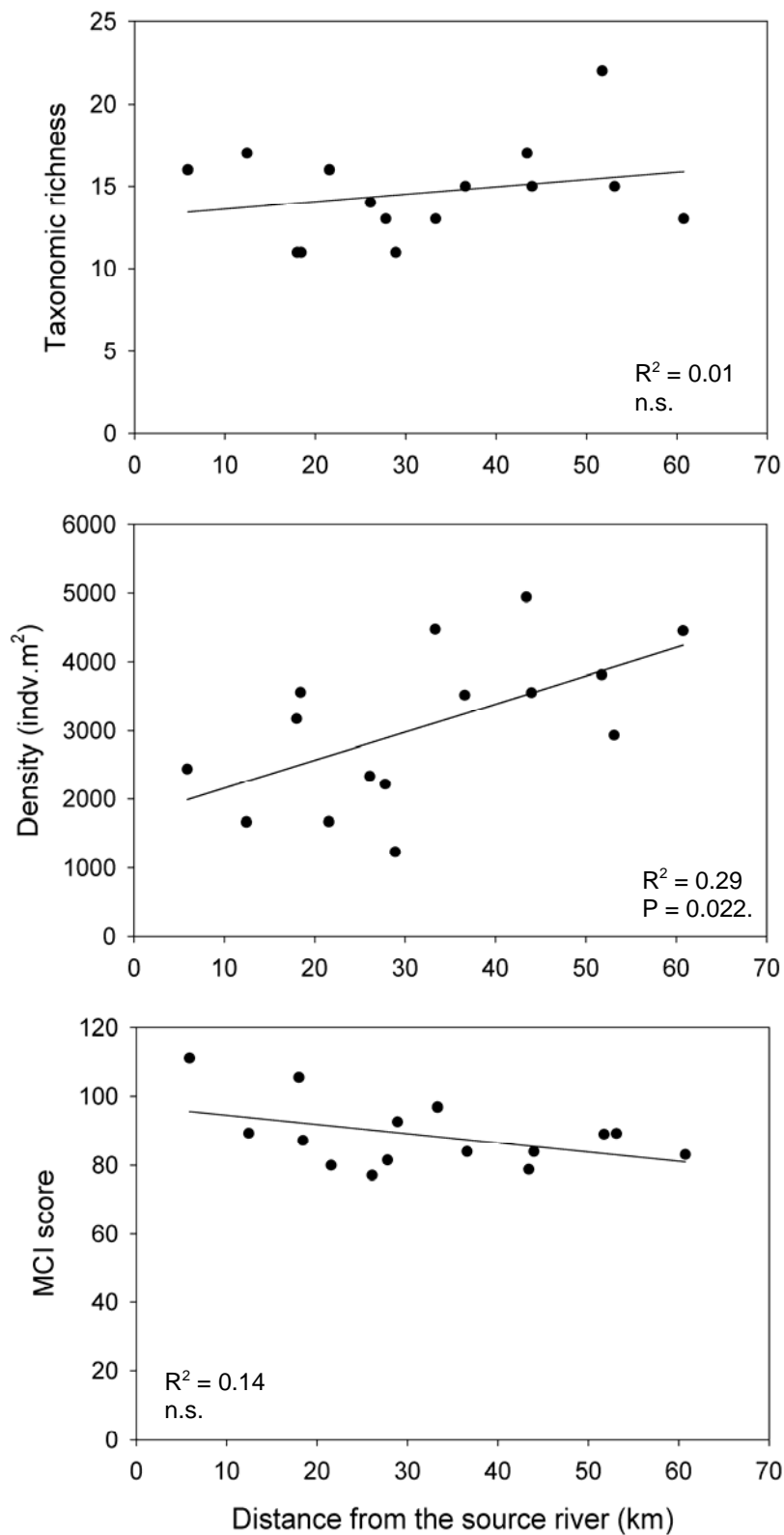


Figure 4. Relationship between distance from the source river and benthic macroinvertebrate taxonomic richness, density (individuals per m²) and MCI score.

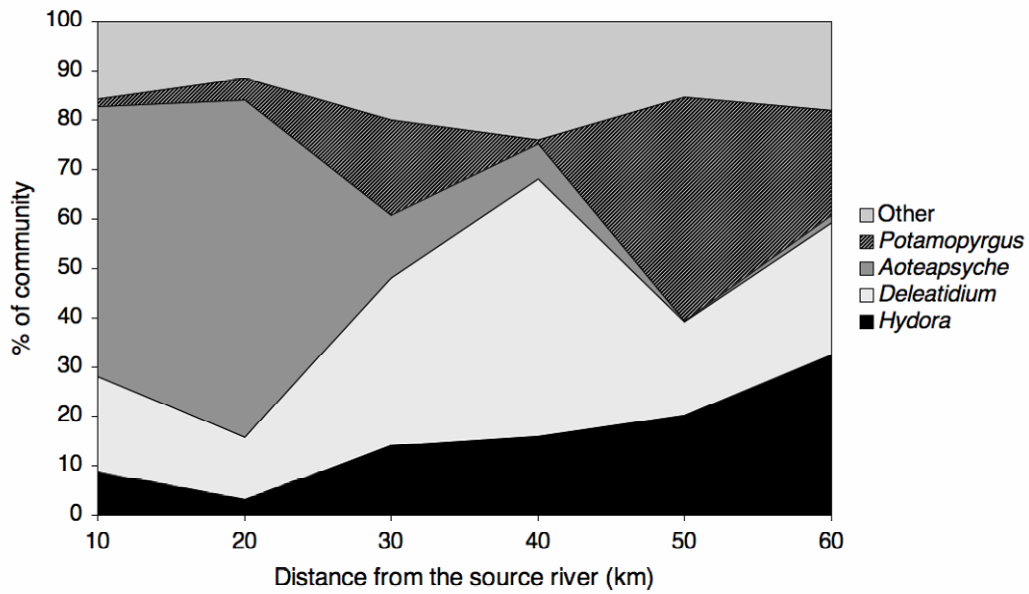


Figure 5. Benthic macroinvertebrate community composition plotted against distance from the source river showing the proportion of the community of the four most common taxa and 'other' taxa.

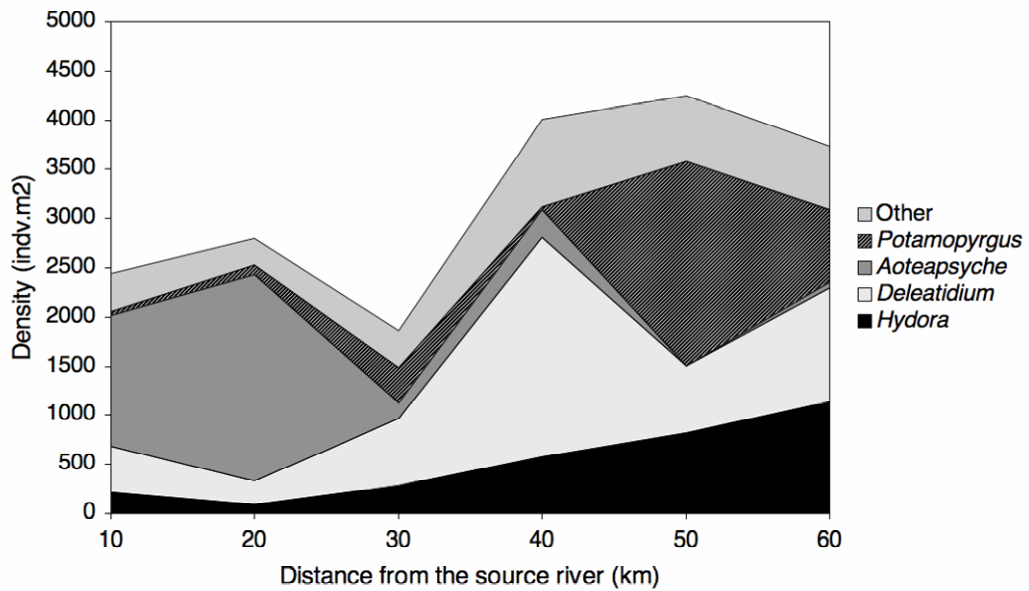


Figure 6. Benthic macroinvertebrate density plotted against distance from the source river showing the densities of the four most common taxa and 'other' taxa.

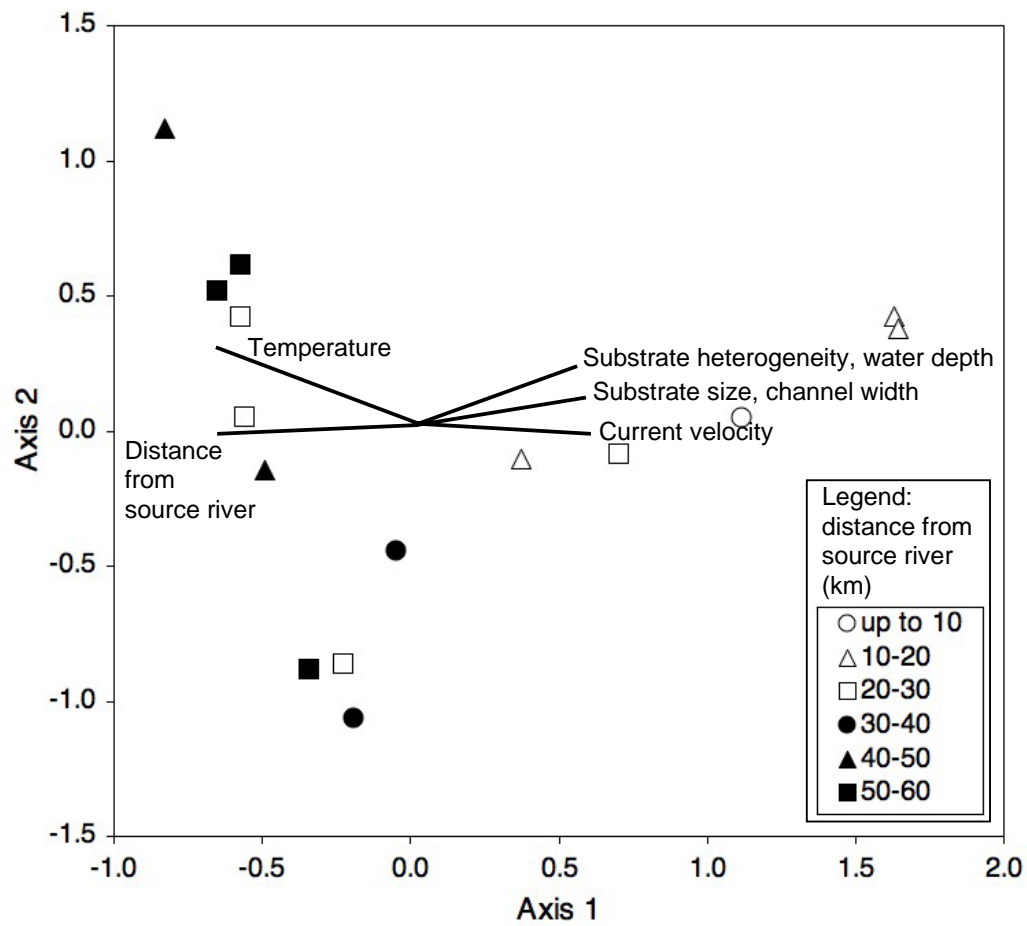


Figure 7. Canonical correlation analysis illustrating the relative abundance of benthic invertebrate taxa in water race sites and the environmental variables associated with their distribution.

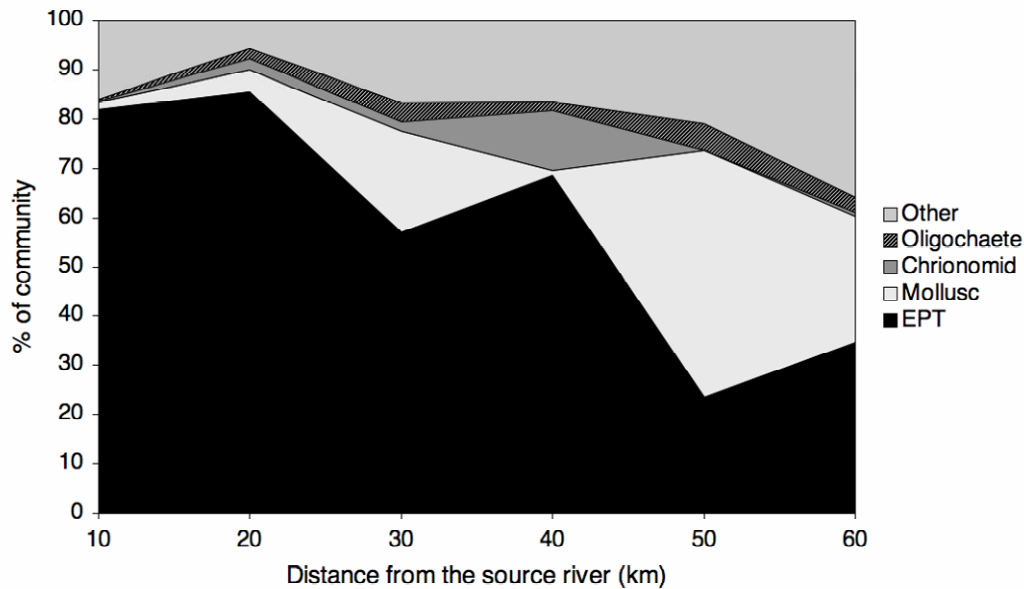


Figure 8. Proportion of the community of pollution intolerant taxa (EPT) and pollution tolerant taxa (oligochaete, chironomid, mollusc), and 'other' taxa plotted against distance from the source river.

Fish communities

Fish communities in stock water races were very depauperate; only three species of fish were caught in the 11 sites: upland bully (*Gobiomorphus breviceps*), brown trout (*Salmo trutta*), and longfinned eel (*Anguilla dieffenbachii*). Upland bully was the most common species, found in 7 sites ranging from the smallest races, with very low flows, to some of the larger races. This species was not found in the one feeder race that was fished, possibly because it was too swift (Jowett & Richardson, 1995). Densities of upland bully ranged from 0.025 to 1.75 per m², with a mean density of 0.37 per m². There was no longitudinal trend in density of upland bully, although only a single fish was present in the two smallest races. Brown trout was found in five sites, in densities ranging from 0.05 to 0.2 per m², and a mean of 0.11 per m². There was also no longitudinal trend in brown trout density, however it was absent from the smaller races in the lower reaches of the network. Longfinned eel was also found in five sites, but in low densities (mean = 0.038 per m², range = 0.025 to 0.05 per m²), and also exhibited no longitudinal trend, although was only found in races with water depth > 0.2 m.

Discussion

Physical and chemical gradients

The physical structure of the stock water race system on the Canterbury Plains contrasts greatly with natural river systems. A ‘typical’ natural dendritic river system begins as a headwater stream, is joined by tributaries, consequently increasing in size to eventually become a large lowland river (Church, 2002). The stock water race network is an inverse dendritic system, with the progressive division of races creating a system of contracting waterways. The frequent rejoining of races further complicates the system, creating a complex network of waterways that criss-crosses the plains.

Because stock water races flow for a relatively short distance through a homogeneous landscape, they do not undergo marked transitions in physical form and primary energy source as would a natural stream shifting from headwaters to a lowland river (Nevins, 1965; Vannote et al., 1980; Statzner & Higler, 1986; Church, 2002). However, the branching structure of the water race system does produce several gradients in physical characteristics. The most obvious of these is their marked decrease in size, specifically channel width and water depth. This decrease in size directly affects other features of the water race channel, including current velocity and temperature.

Substrate size and current velocity, both of which are recognised as critical factors influencing benthic macroinvertebrate communities in natural streams, decreased longitudinally in water races (Hynes, 1970; Minshall, 1984; Jowett & Richardson, 1990; Quinn & Hickey, 1990b; Rempel et al., 2000; Doisy & Rabeni, 2001; Méricoux & Dolédec, 2004; Brooks et al., 2005; Allan & Castillo, 2007). We might therefore expect longitudinal community changes in water races to be influenced by the decreases in substrate size and current velocity. For example, the marked longitudinal decline in the abundance of the net-spinning larva of the caddisfly *Aoteapsyche* sp. observed in the water races could be due to its strong preference for larger, more stable substrate (Quinn & Hickey, 1990b). *Aoteapsyche* also prefers higher current

velocities (Jowett et al., 1991), which it requires to ensure an adequate supply of seston (Georgian & Thorp 1992).

The longitudinal increase in temperature in the water races was probably due to a combination of limited shading and a decreasing volume of water increasing the effects of solar heating. Temperature is often cited as an important factor influencing the structure and function of benthic macroinvertebrate communities in streams (Hynes, 1970; Vannote & Sweeney, 1980; Ward & Stanford, 1982; Allan & Castillo, 2007). Spot temperatures measured in this study were not excessively high, although maximum temperature could easily reach above 25°C in smaller races (Chapter 1). Temperatures of this magnitude could exceed the upper thermal tolerances of some benthic macroinvertebrates (Quinn et al., 1994). For example, stoneflies and mayflies are scarce in rivers where maximum temperature exceeds 19 and 21.5°C respectively (Quinn & Hickey, 1990a).

Natural streams in agricultural landscapes frequently have modified chemical conditions, and these often change downstream as the impacts of agricultural activities accumulate (Harding et al., 1999; Shieh et al., 1999). Turbidity can increase from catchment and stream bank erosion (Quinn et al., 1992; Williamson et al., 1992; Quinn & Stroud, 2002; Riley et al., 2003) and nutrient concentrations (especially nitrogen and phosphorous) often increase from stock effluent and fertiliser application to pasture and crops (Quinn & Stroud, 2002; Riley et al., 2003). Although chemical conditions in the water races were likely to be strongly influenced by agricultural activities, longitudinal gradients in water chemistry were weak. This is probably not surprising, as the water races form a complex network, with races branching and merging frequently. Because smaller races often connect with others, or are recharged with water from larger feeder races, inputs of new water may effectively refresh the water in smaller races. These inputs may dilute turbidity, nutrients and pollutants, consequently reducing the magnitude of gradients in chemical conditions.

Primary energy source

Vannote et al. (1980) proposed that the primary energy source in natural streams changes from mainly terrestrially derived organic matter (CPOM from riparian vegetation) in small headwater streams, to mostly autochthonous primary production

and fine particulate organic matter transported from upstream in the larger downstream sections. This change is thought to be a dominant driver of benthic macroinvertebrate assemblages in streams (Vannote et al., 1980; Hawkins & Sedell, 1981; Baptista et al., 2001). Although there was no longitudinal change in energy source in this study, benthic macroinvertebrate assemblages in the water races were probably influenced by their energy source. The water races had primarily exotic grasses or no vegetation in their riparian zone, a common feature of streams in agricultural areas (Quinn, 2000). Removal of riparian vegetation modifies the primary energy source in streams by reducing inputs of terrestrially derived organic matter and increasing solar energy inputs, consequently increasing the importance of algae as a food source (Quinn et al., 1992; Quinn et al., 1997). Limited shading, high temperatures, and probable nutrient enrichment in water races meant that algal biomass was of a level similar to that common of moderately enriched streams (Biggs, 1996). The relative abundance of macroinvertebrate scrapers (*Potamopyrgus*) and collector-browsers (*Deleatidium* and *Hydora*) in the communities throughout the water race network suggested benthic algae, and other organic matter on the surface of stones, were important energy sources in this system (Winterbourn et al., 1981).

Benthic macroinvertebrates

In natural stream systems, benthic macroinvertebrate community structure responds to the longitudinal gradients in channel morphology and energy sources (Vannote et al., 1980; Hawkins & Sedell, 1981; Cushing et al., 1983; Grubaugh et al., 1996; Baptista et al., 2001). Furthermore, agricultural activities will modify the composition of the communities (Quinn & Hickey, 1990b; Quinn et al., 1992; Scott et al., 1994; Harding & Winterbourn, 1995; Delong & Brusven, 1998; Rickard, 2005). I would therefore expect the benthic macroinvertebrate communities in water races reflected both the impacts of agricultural activities and the morphology of the water race channels.

I did not find strong longitudinal changes to the benthic macroinvertebrate community structure in the water races, aside from the changing abundances of the four most common taxa: *Aoteapsyche*, *Deleatidium*, *Potamopyrgus* and *Hydora*. The benthic macroinvertebrate taxonomic richness of the water races was generally lower than other natural streams in the Canterbury region (Harding, 1994; Harding & Winterbourn, 1995; Wright-Stow, 2001; Rickard, 2005), as the water race

communities comprised just a few common taxa, most of which were generalists in habitat and diet (Winterbourn, 1970; Winterbourn, 1981; Winterbourn et al., 2006). *Deleatidium*, *Potamopyrgus* and *Hydora* were abundant throughout the water race network, including in the smaller more modified downstream reaches. *Hydora* and *Deleatidium* do not have strong substrate size preferences (Quinn & Hickey, 1990b), and *Potamopyrgus* may prefer smaller substrate (Jowett et al., 1991). Also, *Potamopyrgus* and *Hydora* both have high thermal tolerances (Quinn et al., 1994) and are quite tolerant of organic enrichment (Stark, 1993). Therefore, the range of habitat conditions that occurred longitudinally in the water races was probably within the tolerance limits of these generalist taxa, and because they were able to exist in most water races, the magnitude of longitudinal community change was reduced. Only taxa with more specific habitat requirements, such as *Aoteapsyche*, showed longitudinal change. Furthermore, the network structure of the stock water race system, in particular the joining of large races to smaller ones, could have reduced the magnitude of longitudinal patterns in benthic macroinvertebrates. The refreshing effect of ‘new’ water introduced to small races from larger ones may not have only improved chemical conditions in the race, but may have also provided a source of colonists of taxa that were more common in the larger water races.

Fish communities

The fish fauna of the water races was very depauperate, and the presence of only three species indicates that the race environment had low suitability to many fish species. The three species that were present were able to tolerate the modified habitat in the water races, particularly the small substrate and limited riparian cover, although all three were generally absent from the smallest water races. Like the benthic macroinvertebrate communities, the presence of more tolerant fish species restricted the occurrence of longitudinal community change in water races.

Conclusion

Unlike the biological communities of many natural streams, the structure of benthic macroinvertebrate communities of water races did not change in a predictable manner longitudinally. Although the water races showed physical and chemical longitudinal

changes, the defining feature of their habitat, the homogeneity of the instream environment, changed very little. The benthic macroinvertebrate and fish communities of water races were a product of this homogeneous habitat, with communities throughout the water race network comprising a limited set of generalist taxa that were able to tolerate the conditions in most races. In addition, the network structure of the water race system probably keeps many of the smaller races refreshed with cleaner water and reintroduces taxa that are more common in the larger races. This network structure may in fact be important in maintaining diversity in the biological populations in these highly modified waterways. Because many of the streams and small rivers on the Canterbury Plains dry seasonally in their mid-reaches, stock water races probably provide the most extensive network of permanently flowing surface water on the plains. As stock water races can support benthic invertebrate and fish communities throughout the race network, they could provide an important habitat for biodiversity on the plains, although this is limited by their highly modified state.

4

Testing biological responses to habitat heterogeneity: a substrate manipulation experiment

Abstract

Stream habitats that are spatially physically heterogeneous frequently support diverse biological communities. Natural streams typically have a heterogeneous substrate and variable current velocity that create a diversity of microhabitats for benthic invertebrates. However, streams that have been modified by anthropogenic activities will often have degraded habitats. The stock water race system on the Canterbury Plains in New Zealand represents an extreme example of anthropogenic modification to waterways. The water race system is a manmade network of open waterways designed to transport water to farms across the plains. The water race channels are narrow and uniform, with a small, homogeneous substrate and flow consisting solely of riffles and runs. Water races have depauperate macroinvertebrate assemblages, with the communities dominated by a common set of generalist taxa. To investigate the influence of habitat heterogeneity on benthic macroinvertebrate communities, I manipulated habitat in five water races. Large cobbles and small boulders were added to reaches in order to increase habitat diversity. Substrate and current heterogeneity was increased, although this resulted in few significant changes to the benthic macroinvertebrate community. Methodological factors, especially duration and the size of the experimental reach, may have limited the extent of community change. The outcome of this experiment does not eliminate low habitat heterogeneity as a limiting factor for water race communities. Rather, the benthic macroinvertebrate community throughout the water race network is a product of the homogeneous habitat, which limits the availability of colonists of taxa that would benefit from increased habitat diversity in water races.

Introduction

Habitats that are spatially physically heterogeneous generally support a greater biological richness than do structurally simple or extreme habitats (Allan & Castillo, 2007), a pattern that is frequently observed in stream environments (Allan, 1975; Hart, 1978; Flecker & Allan, 1984; Dudley et al., 1986; Scarsbrook & Townsend, 1993; Douglas & Lake, 1994; Beisel et al., 1998; Downes et al., 1998; Beisel et al., 2000; Downes et al., 2000). Physically complex habitats have more habitable space available, and will consequently have a greater number of individuals. An increase in species richness with habitat heterogeneity may therefore simply be caused by a passive increase in the number of species as individuals increase (Downes et al., 2000). However, the pattern is usually considered to be the result of an increase in the diversity of microhabitats in more heterogeneous environments (Douglas & Lake, 1994), allowing resource partitioning and hence coexistence of organisms (Schoener, 1974).

Microhabitats in streams are usually formed by variations in substrate and current velocity. The stream substrate incorporates every object within in the stream channel on which organisms reside (Allan & Castillo, 2007), including inorganic matter, such as silt, cobbles and boulders, and organic material, debris from riparian vegetation and aquatic macrophytes (Giller & Malmqvist, 1998). Substrate heterogeneity is therefore a product of the type of substrates, the range of sizes, and the microhabitats occurring within substrates, such as crevices, ledges, and pits (Hynes, 1970; Minshall, 1984; Douglas & Lake, 1994). Heterogeneity in current velocity occurs at meso- and micro-habitat scales in a natural stream channel due to bed friction, topography and roughness caused by large particles (Allan & Castillo, 2007). Meso-scale variation in current velocity exists from riffle-run-pool complexes, and micro-scale habitat partitioning occurs on or around a single particle; high velocity areas exist on the exposed top of the particle and slower areas occur in the crevices beside and underneath the particle (Giller and Malmqvist, 1998).

Habitat heterogeneity in streams is frequently degraded through human activities such as agriculture, forestry and urbanisation, which often lead to modifications to stream

environments, including channelisation, alteration of substrate, sedimentation, removal of riparian vegetation and flow regulation (Williamson et al., 1992; Delong & Brusven, 1994; Riley, 1998; Jowett, 2000; Suren, 2000; Quinn, 2000; Brasher, 2003; Suren et al., 2005). These modifications often lead to a decline in biological diversity, a change in community structure and alteration of ecosystem function (Quinn et al., 1992; Paul & Meyer, 2001; Negishi et al., 2002; Brasher, 2003; Thompson & Townsend, 2004; Matthaei et al., 2006; Walsh et al., 2007). The stock water race system on the Canterbury Plains in New Zealand represents an extreme example of anthropogenic modification of waterways. The water race system is a network of small, highly modified channels built in the 1880s by early European settlers to transport water to farms across the plains (Logan, 1987). The water races are uniform channels, with small, homogeneous substrate, and flow that consists of riffles and runs, with no pools (Chapter 1). In addition, emergent substrate is rare in races, as water generally fills the entire width of the channel and small substrate predominates. Many freshwater insects require emergent substrate for oviposition (Scarsbrook, 2000). Thus, as oviposition from aerial sources is an important source of recruits in streams (Williams & Hynes, 1976), lack of emergent substrate suitable for oviposition may influence benthic invertebrate communities in water races by limiting the recruitment of a number of aquatic insect species.

Despite the highly modified habitat, water races support a range of benthic macroinvertebrates. However, taxonomic richness is often low, with the communities throughout the race network dominated by a common set of generalist taxa (Chapter 1 & 2). I aimed to test the importance of habitat heterogeneity in influencing benthic macroinvertebrate communities in the stock water races. I manipulated habitat heterogeneity by adding large substrate particles to stock water races to 1) increase substrate heterogeneity by introducing cobbles and boulders to a pebble-dominated substrate, and 2) create depth and velocity variations in an otherwise hydraulically homogeneous channel. I expected increased taxonomic richness and changes to the structure of benthic macroinvertebrate communities to result from the increased physical heterogeneity in the water race channel.

Methods

Study system

There are approximately 6,500 km of stock water races traversing the Canterbury Plains, and as many of the plain's smaller rivers dry seasonally in their mid-reaches, water races probably provide the most extensive network of permanent flowing surface water in the region. The water race system is maintained by four local government authorities: the Waimakariri, Selwyn, Ashburton and Timaru District Councils. Water for the system is sourced from a number of different rivers, streams and springs on the plains. Each water race system includes several large feeder races, which carry water from intakes at local rivers. Smaller lateral races branch off the feeder races, which then often branch to smaller races. Smaller races frequently rejoin to larger races, creating a complex network. The water races flow for roughly 65 km across the plains from the foothills to the coast, ending in sinkholes and drains, with relatively few discharging directly into the ocean.

Experimental design, sample collection and processing

A riffle or run reach in five water races of a similar size (mean width: 80 cm, range: 60-100 cm) were selected from the Selwyn District stock water race network. Initial sampling and substrate addition was carried out in September 2007 and the sites were re-sampled in January 2008. Each of the five sites had a 7 m long upstream control reach and an adjacent 7 m long downstream experimental reach. Four small boulders (250 – 300 mm longest axis) and 10 medium-large cobbles (100 – 250 mm longest axis) were placed randomly along each experimental reach (Fig 1). Water depth and mean current velocity were determined at 10 points in the channel in the control reach (Marsh-McBirney flow mate 2000), and before and after substrate addition in the treatment reach. Substrate size was estimated before and after substrate addition in the treatment reach and in the control reach by measuring the longest axis of 30 randomly selected particles. Substrate was characterised using the Wentworth scale (Cummins, 1962). Water depth and current velocity measurements were repeated in the treatment and control reaches in January 2008.



Figure 1. Photographs showing a stock water race before substrate addition (left) and after substrate addition (right). Photos: Jon Harding.

Benthic macroinvertebrates were collected in three replicate Surber samples (0.09 cm^2 , $500 \text{ }\mu\text{m}$ mesh) at random locations in the treatment (before substrate addition) and control reaches in September 2007, and again in the treatment and control reaches in January 2008. Samples were preserved in 90% ethanol in the field, sieved in the laboratory with a $500 \text{ }\mu\text{m}$ sieve, and sorted and identified to the lowest taxonomic group possible in the laboratory using the keys of Winterbourn et al. (2006) and Winterbourn (1973).

Data analysis

The physical and biological data were tested using ANOVA to investigate differences between treatments and sampling dates. Paired *t*-tests were used to test for differences in either the treatments or controls between sampling dates, and two-sample *t*-tests were used to test for differences between the treatment and control at either sampling date. Data was log or square root transformed if it was not normally distributed. Mann-Whitney U tests were used for data that could not be transformed satisfactorily. Significant differences for all analyses were accepted at $P < 0.05$. Heterogeneity of substrate, current velocity and water depth were represented by the standard error of the mean and the range (maximum minus minimum value). Detrended correspondence analysis (DCA) was used to assess the distributions of taxa abundance amongst treatments and sites using PC-ORD (McCune & Mefford, 1999).

Results

Physical

Addition of cobbles and boulders significantly increased average substrate size in the post-addition treatment compared to the pre-addition treatment and control (Table 1). Minimum substrate size was the same in the pre-addition treatment, post-addition treatment and control. However, maximum substrate size was significantly greater in the post-addition treatment (Table 1). Substrate heterogeneity also increased after the addition of large substrate; the standard error and range were significantly higher in the post-addition treatment compared to the pre-addition treatment and control (Table 1). At the final sampling, areas of fine sediments occurred on the downstream side of the larger boulders in some of the treatment reaches.

Average current velocity was slightly but not significantly lower in the post-addition treatment compared to the pre-addition treatment and control (Table 1). Current velocity variation (standard error and range) was significantly greater in the post-addition treatment than the pre-addition treatment and control (Table 1). Minimum current velocity was significantly lower in the post-addition treatment compared to the pre-addition treatment and control, with near-stationary water present in the post-addition treatment (Table 1).

Average water depth was slightly but not significantly greater in the post-addition treatment compared to the pre-addition treatment and control (Table 1). Although depth was only approximately 2.5 cm greater in the post-addition treatment, it represented a 36% increase in depth from the pre-addition treatment. Water depth variation was slightly but not significantly greater in the post-addition treatment than the pre-addition treatment and control (Table 1). After a greater length of time than the study period, scouring and deposition from the variation in current velocity may have created depth variations.

Table 1. Substrate size, current velocity and water depth in the pre- and post-addition treatment and control. Pre-addition treatment values are from the initial sampling and post-addition treatment and control values are from the final sampling. Statistics are *t*-test, $P < 0.05$. Significance codes: n.s. non significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

	Pre-addition treatment	Post-addition treatment	Control	Post- vs. pre-addition treatment	Post-addition treatment vs. control
<i>Substrate size (cm)</i>					
Mean	20.1	38.5	22.9	***	**
Standard error	3.1	12.1	3.7	***	***
Minimum	0.1	0.1	0.1	n.s.	n.s.
Maximum	68.2	266.0	79.0	***	***
Range	68.1	265.9	78.9	***	***
<i>Current velocity (ms^{-1})</i>					
Mean	0.32	0.25	0.31	n.s.	n.s.
Standard error	0.03	0.06	0.03	*	*
Minimum	0.22	0.01	0.18	*	*
Maximum	0.48	0.51	0.43	n.s.	n.s.
Range	0.26	0.49	0.25	*	*
<i>Water depth (cm)</i>					
Mean	7.2	8.6	7.1	n.s.	n.s.
Standard error	0.5	0.6	0.4	n.s.	n.s.
Minimum	5.2	5.8	4.8	n.s.	n.s.
Maximum	9.5	11.7	9.0	n.s.	n.s.
Range	4.3	5.9	4.2	n.s.	n.s.

Benthic macroinvertebrates

A total of 30 benthic macroinvertebrate taxa were found in the five reaches. Average taxonomic richness for all sites and treatments was 8.9 (SE \pm 0.3, range: 5–14). There was no significant difference in taxonomic richness between the treatment and control at either the initial or final sampling (Fig. 2). However, a small decrease in richness in the control and an increase in the treatment meant treatment richness was marginally higher than control richness at the final sampling. However, there were a greater total number of taxa represented across all five treatment reaches ($n = 27$), than in all five

control reaches ($n = 21$) at final sampling. A comparable number of taxa were found across all five sites in the treatment and control reaches at the initial sampling ($n = 21$ and 23 respectively). Also, two taxa more common to lentic waters, *Aeshna brevistyla* and *Austrolestes* sp. (Odonata), appeared only in the treatments at the final sampling.

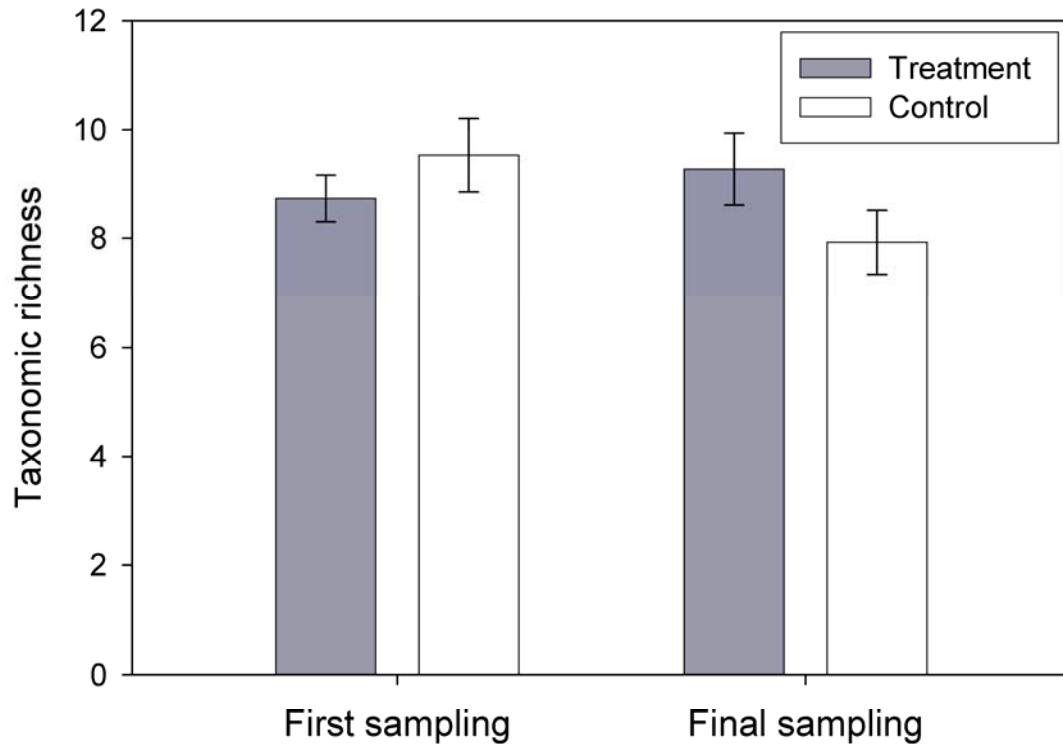


Figure 2. Mean ($\pm 1SE$) taxonomic richness of benthic macroinvertebrates in the pre-addition treatment and control at the first sampling and the post-addition treatment and control at the final sampling.

The density of benthic macroinvertebrates in the treatment and control did not differ at the initial sampling date (Fig. 3). Density increased significantly in the control between the initial and the final sampling (t -test, $P = 0.01$), and in the treatment, although this was not significant (t -test, $P = 0.07$) (Fig. 3). Density was significantly higher in the control than in the treatment at the final sampling (t -test, $P = 0.0006$). The increase in density in the treatment and control was caused by an increase in the abundance of about half of the taxa.

The average community composition of the five sites varied very little between the treatment and control at either sampling date (Fig. 4). An ordination of relative abundance of benthic macroinvertebrates indicated the sites had different community compositions to each other (Fig. 5). However, only two of the five sites had community compositions that differed between treatments and/or sampling dates (sites 2 and 3), but these showed no obvious pattern (Fig. 5). Of interest, at the end of the experiment several of the boulders in the treatment reaches possessed Trichoptera pupa cases, egg masses, macrophytes and filamentous algae. All of which were absent or uncommon on the typical water race substrate in both the treatment and control reaches.

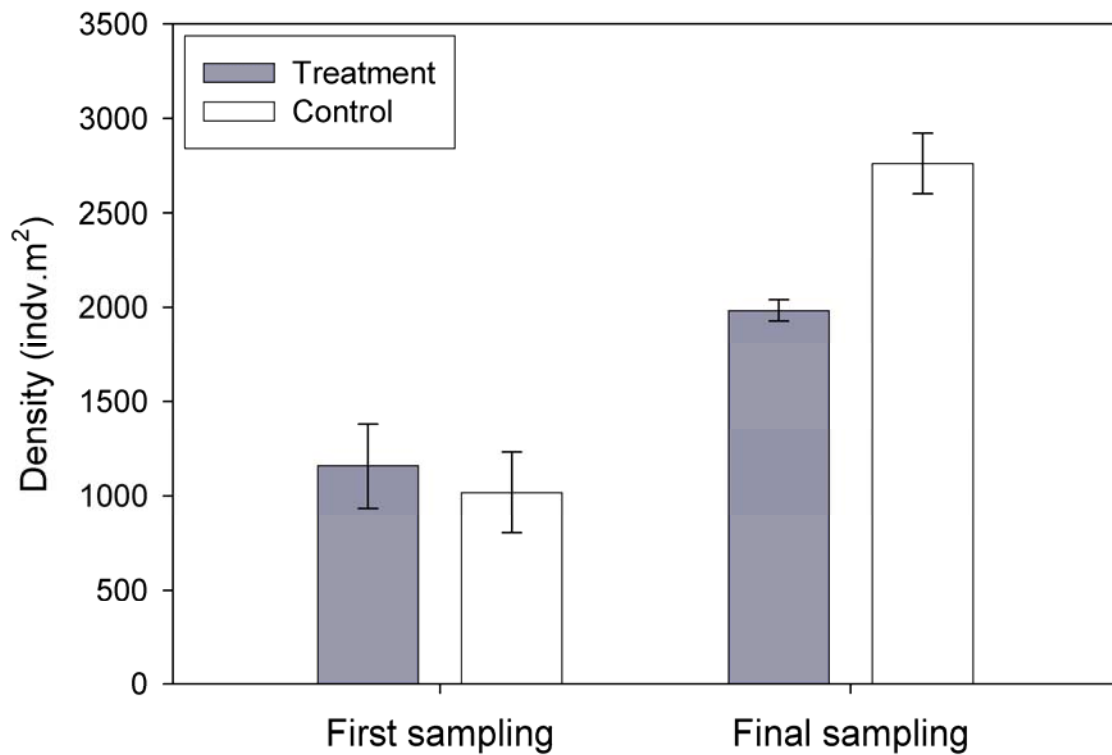


Figure 3. Mean ($\pm 1SE$) macroinvertebrate density (individuals per m²) in the pre-addition treatment and control at the first sampling and the post-addition treatment and control at the final sampling.

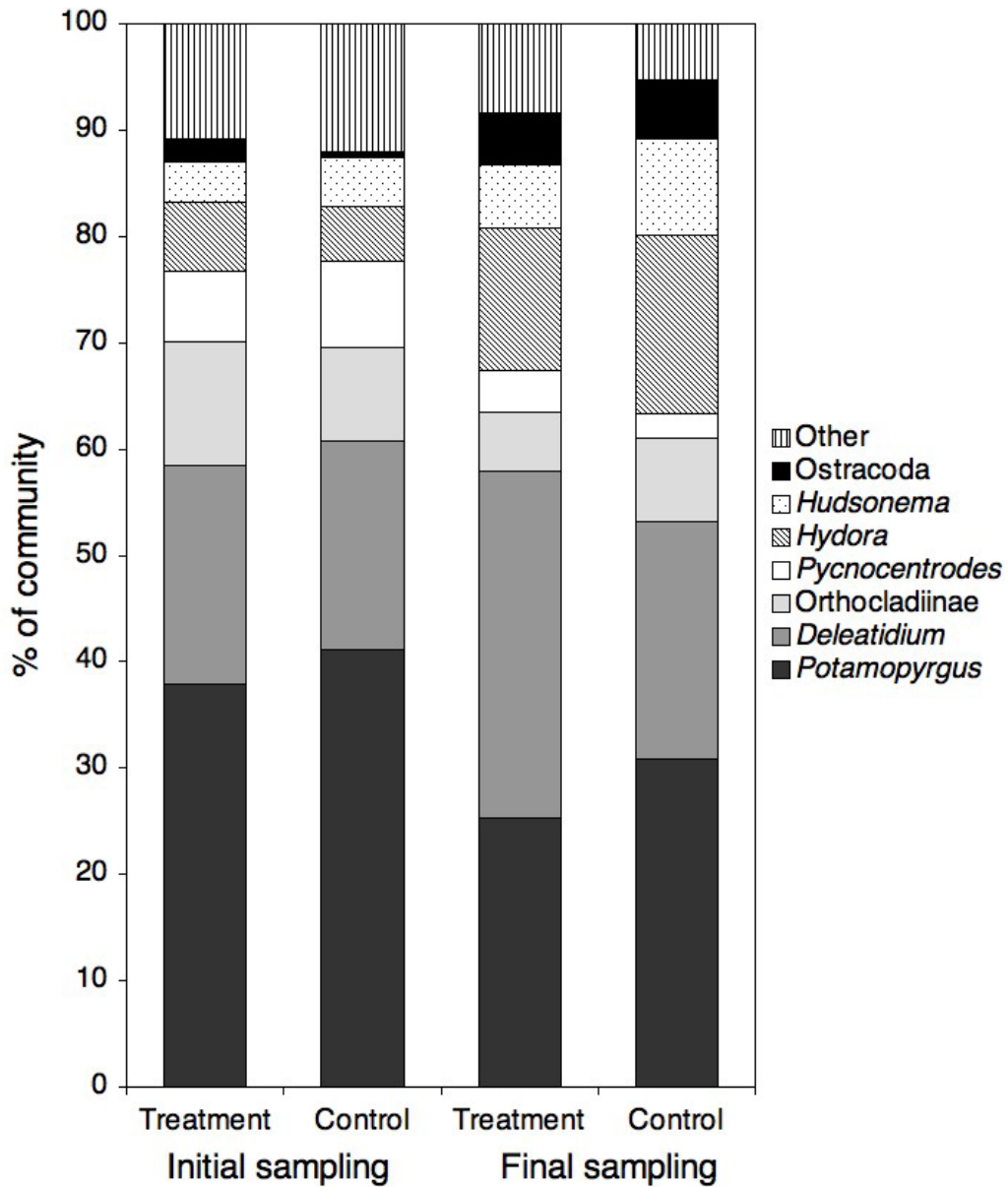


Figure 4. Mean benthic macroinvertebrate community composition of the treatment and controls at the initial and final sampling.

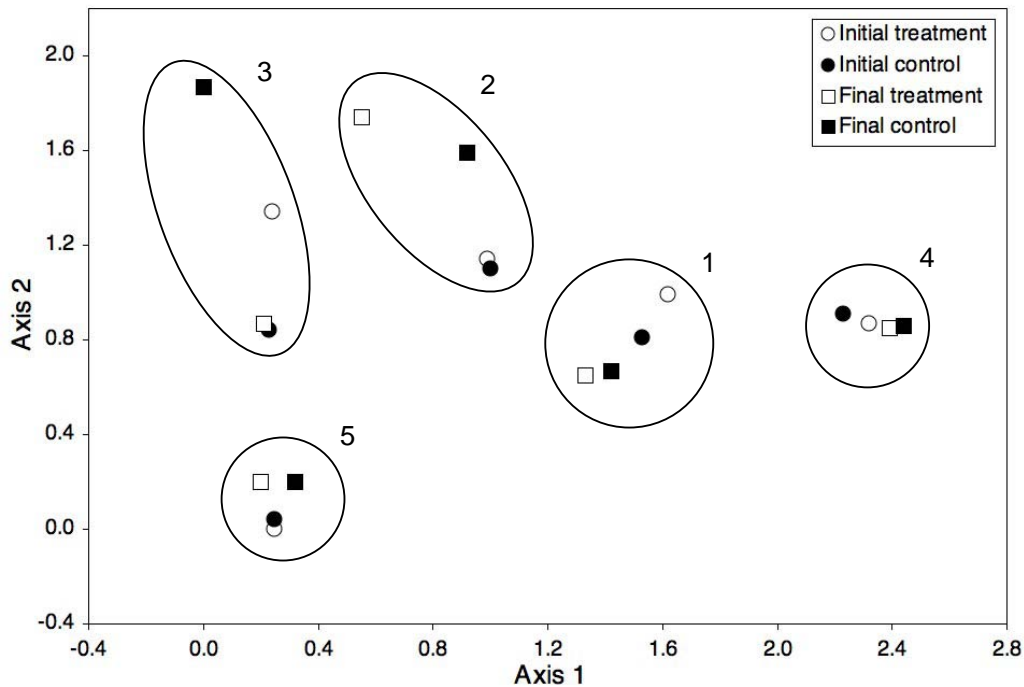


Figure 5. Detrended correspondence analysis illustrating the relative abundance of benthic macroinvertebrate taxa in the five water race sites (numbered 1 – 5) in the treatment and controls at the initial and final sampling.

Discussion

The stock water race system was designed with the sole purpose of transporting water from rivers to farms across the Canterbury Plains. The water races are narrow and channelised, with a homogeneous, pebble-dominated substrate, and uniform current velocity. In this experiment I increased substrate heterogeneity in the water races with the addition of boulders and large cobbles. Larger, more heterogeneous substrate often promotes a greater abundance and taxonomic richness of benthic invertebrates in natural streams (Hynes, 1970; Allan, 1975; Williams, 1980; Flecker & Allan, 1984; Minshall, 1984; Beisel et al., 1998; Beisel et al., 2000; Boyero, 2003). In addition, many invertebrates show preferences for larger particles (Cummins & Lauff, 1969; Quinn & Hickey, 1990b; Jowett et al., 1991), probably because they require greater current velocities to disturb them and therefore provide a more stable habitat for both periphyton and invertebrates (Quinn & Hickey, 1990b). Larger substrates also trap and retain more coarse particulate organic matter which provides additional habitat and a food source for many taxa (Rounick & Winterbourn, 1983).

Meso-scale variation in current velocity was also increased after substrate addition, and the large substrate also increased the current velocity variations at the micro-scale (the scale at which current affects macroinvertebrates; Hart & Finelli, 1999), through an increase in the bed roughness caused by large particles (Allan & Castillo, 2007). In natural streams, numerous benthic invertebrates show current velocity preferences (Eddington, 1968; Wellnitz et al., 2001; Jowett, 2003; M rigoux & Dol dec, 2004; Brooks et al., 2005). For example, filter feeders, such as net-spinning caddisfly larvae, prefer higher current velocities to ensure an adequate supply of seston (Georgian & Thorp, 1992), and some species need the highly oxygenated water found in high velocity areas (Quinn & Hickey, 1990b). Other species, such as collector-gatherers, prefer the slower current velocities that promote the accumulation of detritus (Jowett, 2003). Consequently, micro- and meso-scale heterogeneity in current velocity should allow a greater number of species to find a satisfactory habitat regardless of average channel current velocity (Jowett & Richardson, 1990).

Despite the increase in physical heterogeneity in the water races from the addition of substrate, very few significant changes to the structure benthic macroinvertebrate community were found. Average taxonomic richness did not change significantly, although richness was slightly increased in the substrate addition reaches at the final sampling. Also, the five substrate addition reaches had a greater total number of taxa present than did the control reaches at the final sampling. For example, two lentic taxa (*Aeshna brevistyla* and *Austrolestes* sp.) occurred only in substrate addition reaches, suggesting that there may have been some increase in the range of habitats available in these reaches.

I propose a number of potential reasons as to why there was no significant effect of increased physical heterogeneity on the benthic macroinvertebrate communities. Firstly, the time between initial and final sampling (4 months) may have been too short for a noticeable community change to occur. Taxa might have colonised via downstream drift in this time (Brittain & Eikeland, 1988), but it is unlikely new taxa would have arrived via aerial colonisation. The occurrence of egg masses on the boulders at the end of the experiment suggested that the boulders provided oviposition sites that were otherwise absent from water races. If the experiment had been run for 9–12 months it may have been more likely to cover the full insect lifecycle (most

Ephemeroptera and Trichoptera have a 1-year life cycle; Winterbourn, 2004), and new taxa that arrived via aerial colonisation should have been apparent in the benthos after this time.

Secondly, an experimental reach length of 7 m reach may have not been large enough. New taxa that might have colonised the treatment reaches could have been lost through downstream drift in reaches of this length, as many benthic invertebrates drift up to several metres during their aquatic larval stage (Brittain & Eikeland, 1988). Although some benthic invertebrates can drift 10s–100s of metres (Brittain & Eikeland, 1988), increasing reach length would have reduced the chance of newly colonised invertebrate taxa being lost through drift.

Third, the cobbles and boulders added may have been too large to increase substrate heterogeneity in a useable way for benthic macroinvertebrates. Although the range of substrate sizes was increased, with gravel- to boulder-sized particles present, there were few intermediate (small-medium cobble) sizes. Also, the boulders were fairly smooth and may have had low habitat suitability to many taxa. A number of studies investigating the effect of roughness of natural and artificial substrate have revealed fewer species and individuals reside on smooth substrates compared to rough substrates (Hart, 1978; Douglas & Lake, 1994; Downes et al., 1998; Downes et al., 2000). Addition of a range of cobble sizes as well as boulders and large cobbles, or substrates with surface roughness, may have been a more effective way to increase substrate heterogeneity in the water races.

Finally, there are a number of biotic factors that may have prevented an effect of the heterogeneity manipulation. This experiment relied on new taxa colonising the treatment reaches, and on the presence of taxa that would be favoured by addition of habitats associated with large substrate. Although some benthic macroinvertebrate taxa show substrate size preferences, many are equally found on stones of all sizes (Allan & Castillo, 2007). The taxa present in water races may have little or no preference for particular substrate size, or may even prefer small substrate, and thus may not have been affected by addition of large particle habitats. This feature of the macroinvertebrate fauna, combined with the possible low habitat suitability of the

boulders, may explain the lower benthic macroinvertebrate density in the substrate addition reaches compared to the controls that was found in this study.

Benthic macroinvertebrates can colonise new reaches via downstream drift and/or aerial dispersal (Williams & Hynes, 1976). However, in this study, arrival of new taxa to the treatment reaches depended on the nearby waterways having different taxa. Benthic macroinvertebrate taxonomic richness was low at all sites, and may have been similar in the surrounding water races. The highly modified and homogeneous nature of the water races has produced a benthic macroinvertebrate community throughout the race network that is dominated by a limited set of taxa (Chapters 1 & 2). Therefore, the nearby water races probably provided a very limited pool of potential new colonists. It was possible that new taxa from other waterways on the plains could colonise the water races via aerial dispersal (Williams & Hynes, 1976). However, as adult aquatic insects tend to travel 10s-100s of metres from the stream they emerged from (Kovats et al., 1996; Collier & Smith, 1997; Petersen et al., 1999; Briers et al., 2002; Petersen et al., 2004), other waterways may have been too far away to provide a source of colonists for the water races.

Conclusion

Although no significant changes were observed in the benthic macroinvertebrate communities after an increase in habitat heterogeneity in the water races, it does not exclude the possibility that the benthic macroinvertebrate communities in water races are limited by homogeneous habitat. Aside from possible design limitations of this study, the lack of colonists available to the experimental reaches was likely to be a significant factor limiting the effect of an increase in habitat heterogeneity in water races. Like many stream restoration projects, this experiment was based on the ‘field of dreams’ hypothesis (Palmer et al., 1997) (i.e. if you build it, they will come), with a belief that an increase in habitat heterogeneity should be followed by an increase in biological richness (Bond & Lake, 2003). Many stream restoration projects attempting to increase taxonomic richness or alter the structure of aquatic communities by changing stream habitat have also met with limited success (Larson et al., 2001; Parkyn et al., 2003; Bernhardt et al., 2005; Suren & McMurtrie, 2005). A

number of factors prevent stream restoration from working in practice very often, but colonisation barriers have been found to be one of the most important (Bond & Lake, 2003).

The stock water race system may provide an important habitat for freshwater biodiversity on the Canterbury Plains (Chapters 1 & 2), although its value is limited by its highly modified, homogeneous environment. An increase in the diversity of the benthic macroinvertebrate communities in water races could improve the biodiversity value of the stock water race network. The slight increases in taxonomic richness and the occurrence of egg masses on boulders in substrate addition reaches found in this study suggests an increase in habitat heterogeneity in water races may produce an increase in taxonomic richness and changes to the community structure. However, significant changes to benthic macroinvertebrate assemblage probably require a greater length of time, a larger area of manipulation and a more variable range of particle sizes.

5

Fish communities of a highly modified waterway in an agricultural landscape

Abstract

Freshwater systems worldwide have been impacted by agricultural activities through the modification and degradation of in-stream habitats. Reduced diversity and altered fish assemblage structure have been well documented in streams in agricultural catchments. The Canterbury Plains in New Zealand is one of the most intensively farmed regions in the country. Increases in water abstraction to support the intensification of agricultural activities have altered the flow regimes of natural waterways on the plains, with many of the streams and small rivers seasonally ephemeral or experiencing significant drying reaches. Agricultural intensification on the plains has also led to the development of a network of shallow, channelised, open water races to transport water for stock. The stock water race system consists of approximately 6,500 km of races, and is probably the most extensive permanent lotic ecosystem in the region. This study examined the importance of the water races as habitat for fish biodiversity and as a refuge for fish species. Thirty-eight water race and 11 natural stream sites were sampled by three pass electric shocking, and 89% (34) of the water races and 91% (10) of the natural streams contained fish. Two species, upland bully (*Gobiomorphus breviceps*: Eleotridae) and introduced brown trout (*Salmo trutta*: Salmonidae), were commonly found in water races, and the average species richness of the water races was 1.5. The natural streams had four commonly occurring fish species (*G. breviceps*, *S. trutta*, *Anguilla dieffenbachia* [Anguillidae], and *Galaxias vulgaris* [Galaxiidae]) and an average species richness of three. In general, diadromous fish species were absent from the water race system as races rarely flow to the sea. Non-diadromous galaxiids were also absent from water races. The highly modified and homogenous environment in water races combined with the presence of brown trout may reduce fish diversity and exclude many likely fish colonist species.

Introduction

Expansion and intensification of agricultural land is a global phenomenon, and is recognised as one of the most important human modifications to freshwater ecosystems (Matson et al., 1997; Pimentel et al., 1997; Richter et al., 1997; Lemly et al., 2000; Naiman & Turner, 2000; Postel, 2000; Foley et al., 2005). Agricultural activities, particularly those involving forest clearing, can cause habitat degradation and loss in freshwater systems through the over use of water resources and alteration of stream habitats, including light levels, water temperature, stream bed characteristics, bank stability, and increases in nutrient concentrations from the application of fertilisers and agricultural chemicals, and the discharge of stock effluent (Morgan & Graynoth, 1978; Graynoth, 1979; Soulé, 1991; Allan & Flecker, 1993; Harding & Winterbourn, 1995; Rapport & Whitford, 1999; Postel, 2000; Quinn, 2000). These habitat modifications can have considerable effects on freshwater fish (Maitland, 1995), and studies worldwide have documented altered fish assemblage structure and reduced species diversity in streams in agricultural catchments (Karr et al., 1985; Hanchet, 1990; Minns, 1990; Jones et al., 1999; Walser & Bart, 1999).

The Canterbury Plains on the east coast of New Zealand has been one of the most intensively farmed regions in the country since it was colonised by European settlers in the 1840s (Wood & Brooking, 2001). Even before the arrival of European farmers, the Canterbury Plains was subject to substantial alteration with the burning of the original podocarp forest by the indigenous Māori (McGlone, 1989). Since European settlement, sheep farming and mixed cropping have been the primary agricultural activities, however recent market shifts have led to dramatic growth in intensive dairying (Smith & Montgomery, 2004; ABARE & MAF, 2006). Increases in water abstraction to support the intensification of agricultural activities have altered the flow regimes of natural waterways on the plains (Taylor & Smith, 1997; Morgan et al., 2002), with many of the streams and small rivers seasonally ephemeral or having significant drying reaches (Datry et al., 2007; Larned et al., 2008). In addition, numerous studies of New Zealand streams and rivers, including some from the Canterbury Plains, have found the degree of agricultural development of catchments

has a strong relationship with lowered water quality and reduced biodiversity of stream fauna (Hanchet, 1990; Quinn & Hickey, 1990b; Harding & Winterbourn, 1995; Wilcock et al., 1999; Wright-Stow, 2001; Meredith & Hayward, 2002; Jowett & Richardson, 2003; Thompson & Townsend, 2004; Rickard, 2005).

However, this same agricultural intensification on the Canterbury Plains has led to the development of a network of permanently flowing artificial water races. Water availability has always been a limiting factor for farmers on the Canterbury Plains, where annual rainfall is low (approximately 625 mm/year; Fitzharris et al., 1992), and summers are frequently hot and dry (de Lisle, 1969). To improve water supply and increase agricultural production early European settlers constructed a network of open water races to provide stock and domestic water to farms across the plains. Although it was built over 120 years ago, and many farmers have since switched to aquifer bores to supply water, the stock water race system is still widely used today. As there are approximately 6,500 km of stock water races traversing the plains, the water race network provides a very extensive permanent lotic ecosystem in the region. However, race channels provide a highly modified and homogeneous habitat, with uniform, shallow channels, low flow variability and small, homogeneous substrate (Chapter 1).

The loss of habitat due to the drying of natural streams across the Canterbury Plains has caused the local fish populations to become patchy and disjunct in distribution (McDowall, 1990). Hence the stock water race system may provide an important permanent freshwater habitat and potential refuge to many stream species. In this study, I characterised the fish fauna of the water race system and compared race communities to those in natural streams to determine the importance of the water races to the maintenance of fish species in the Canterbury Plains.

Methods

Study system

The Canterbury Plains dominate the central east coast of the South Island of New Zealand, and comprise the largest flat area in the country, being approximately 180 km long by 70 km wide (Fitzharris et al., 1992). The Canterbury Plains are bounded by the foothills of the Southern Alps to the west, and the Pacific Ocean to the east. The region's stock water race network is maintained by four local government authorities: the Waimakariri, Selwyn, Ashburton and Timaru District Councils. Water for these systems is sourced from a number of different rivers, streams and springs. Each system includes several large feeder races, which carry water from intakes at local rivers. The feeder races supply a complex array of smaller lateral races, which then often supply further smaller tributaries. Thus, unlike natural river systems, the water races become smaller downstream. The water race network is further complicated by the frequent joining of small races to larger lateral or feeder races. The water races flow for roughly 65 km across the plains from the foothills to the coast, ending in sinkholes and drains, with relatively few discharging directly into the ocean.

In this study, a total of 38 race sites were selected from the four districts (Fig. 1). A range of water race sizes was sampled, from large feeder races near the foothills to smaller races near the coast. Difficulties accessing races on private property meant that most sites were located where races crossed or ran alongside public roads. Eleven sites in 2nd – 4th order natural streams were also sampled to allow the comparison of fish faunas between similar sized natural and artificial systems. These streams and small rivers were all in the vicinity of the stock water race systems, however included a wide range of stream types, including streams near the foothills, small ephemeral rivers, coastal springs and spring tributaries of large braided rivers.

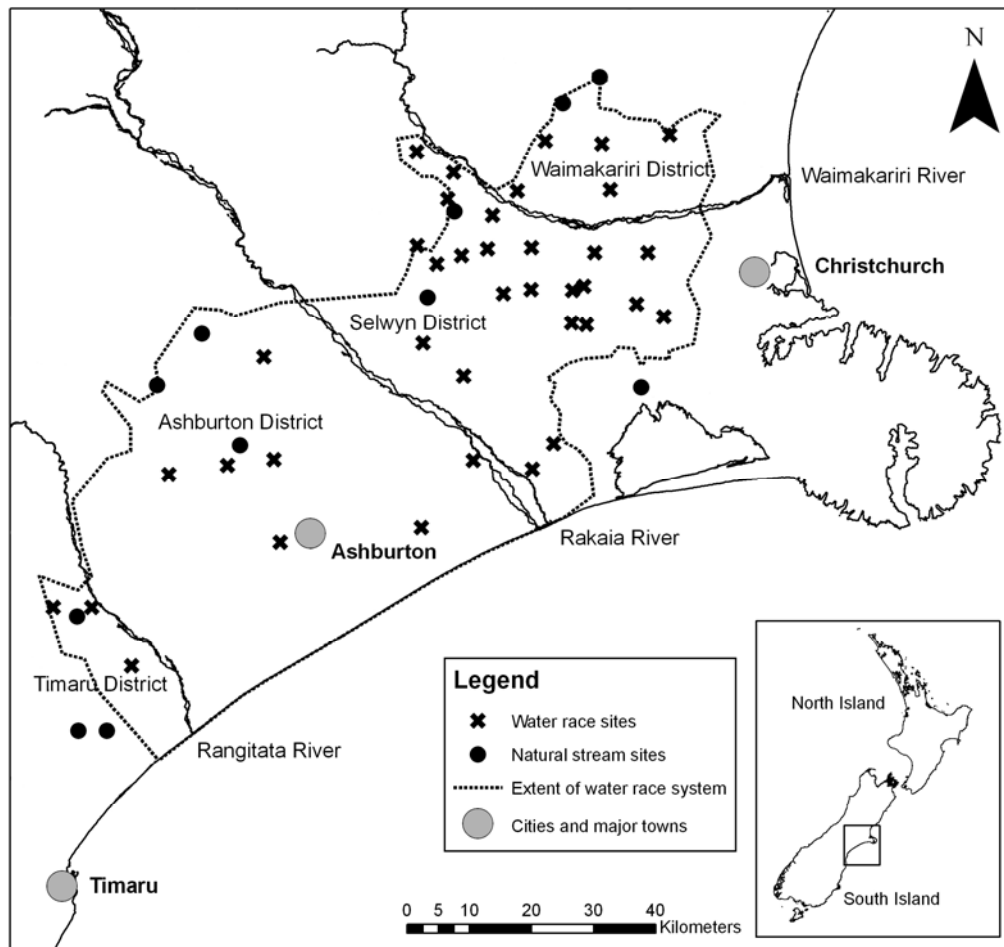


Figure 1. Map showing the 38 water race sites and 11 natural stream sites sampled on the Canterbury Plains.

Sampling methods

All sites were sampled on a single occasion during the austral summer of 2007 or 2008. A range of physical and chemical parameters was collected at each site. Each site consisted of a reach of 20 m and as pools are essentially absent in stock water races, all sites selected were in riffle-run complexes. At each site, mean current velocity and depth were determined at three different points across a transect (Marsh-McBirney flow mate 2000), and channel width at water level was measured. Mean substrate size and substrate heterogeneity was estimated by measuring the longest axis of 30 randomly selected particles. Substrate heterogeneity was estimated using the standard error of the mean of the 30 particles. Bank and channel stability was assessed using the subjective channel evaluation method described by Pfankuch (1975), where a reach score of <38 is excellent; 39-76, good; 77-114, fair, and >115, poor. Spot

measurements of water temperature and chemical parameters including conductivity and dissolved oxygen (DO) were taken in the field using standard meters (Oakton pH/CON10 and YSI 550A). Turbidity (NTU) was measured in the laboratory using a portable Hach turbidimeter 2100P.

Sites were electric fished using a Kainga backpack electric fishing machine (EFM300; NIWA Instrument Systems, Christchurch, New Zealand) in a 20 m reach using the 3 pass removal technique. Fish were counted and identified live in the field to species according to McDowall (2000) and released.

Data analysis

Data for all physical, chemical and biotic characteristics of water races and natural streams was compared using two sample t-tests. Data was log or square root transformed if it was not normally distributed. Mann-Whitney U tests were used for data that could not be transformed satisfactorily. Correlations between fish densities and physical and chemical parameters were tested using Pearson correlation analysis. Significant differences for all analyses were accepted at $P < 0.05$.

Results

Notable habitat differences between the water races and natural streams were channel width, substrate size and substrate heterogeneity, all of which were significantly lower in water races (Table 1). The Pfankuch index of channel stability was significantly higher in water races, indicating they had less stable channels than natural streams (Table 1). However, the mean channel stability of both water races and natural streams was classed as 'good'. Temperature, conductivity and DO were not significantly different between water races and natural streams, although turbidity was significantly higher in water races (Table 1).

Table 1. Physical and chemical parameters for water races and natural streams sampled in the Canterbury Plains (water races $n = 38$, natural streams $n = 11$). Statistics are t-test, $P < 0.05$. Significance codes: n.s. non significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Water race		Natural stream		<i>t</i> -stat	<i>P</i>
	Mean (1SE)	Range	Mean (1SE)	Range		
<i>Physical</i>						
Channel width (m)	1.1 (0.05)	0.6 – 2.0	4.4 (0.52)	2.0 – 7.3	11.686	***
Depth (m)	0.17 (0.01)	0.07 – 0.38	0.18 (0.01)	0.11 – 0.24	0.116	n.s.
Current velocity (ms ⁻¹)	0.52 (0.04)	0.15 – 1.09	0.56 (0.12)	0.16 – 1.32	0.386	n.s.
Substrate size (cm)	2.8 (0.14)	1.0 – 4.5	6.9 (0.66)	3.7 – 9.6	9.363	***
Substrate heterogeneity (SE of mean size)	0.43	0.18 – 1.02	0.72	0.35 – 0.99	4.208	**
Channel stability (Pfankuch)	64 (1)	54 – 84	55 (4)	42 – 77	4.208	**
Temperature (°C)	17.2 (0.5)	11.6 – 24.2	17.4 (0.7)	13.4 – 21.0	0.161	n.s.
<i>Chemical</i>						
Conductivity (µS @ 25°C)	71 (7)	12 – 217	89 (9)	58 – 157	1.375	n.s.
DO (mg/L)	10.2 (0.2)	7.1 – 11.9	10.7 (0.4)	8.9 – 12.8	1.497	n.s.
Turbidity (NTU)	9 (0.9)	0.9 – 32.4	2 (0.5)	0.6 – 5.5	4.773	***

Of the 38 water race sites fished, 34 (89%) contained fish, and 10 of the 11 (91%) natural streams contained fish. Four species of fish were caught in stock water races: upland bullies (*Gobiomorphus breviceps*: Eleotridae), brown trout (*Salmo trutta*: Salmonidae), longfinned eels (*Anguilla dieffenbachia*: Anguillidae) and torrentfish (*Cheimarrichthys fosteri*: Pinguipedidae). Whereas seven species were found in natural streams; these included the species collected in water races as well as common bullies (*G. cotidianus*), bluegill bullies (*G. hubbsi*) and Canterbury galaxias (*Galaxias vulgaris*: Galaxiidae). Upland bullies were the most common species in both the water races and natural streams (Table 2), and did not differ significantly in abundance between the two (Mann-Whitney U test, $P = 0.39$). Brown trout was the second commonest species in water races, and tended to occur in higher densities in the water races than in the natural streams (Table 2), although this was not significant (Mann-Whitney U test, $P = 0.39$). Brown trout were rare in the Waimakariri race system as a screen on the water intake in the Waimakariri River limits fish access to the system. One longfinned eel and one torrentfish were found among the 38 race sites (Table 2). Canterbury galaxias was found in five of the natural streams, longfinned eel in four and common bully, bluegill bully and torrentfish occurred in one natural stream site each (Table 2).

Table 2. Number and percent of each fish species per site and the mean and range of densities of each fish species in water races and natural streams sampled in the Canterbury Plains (Mean \pm 1SE; water races n = 38, natural streams n = 11). Mean density and range of densities were calculated only from the sites that the species was present at.

	Water race			Natural stream		
	No. sites (%)	Mean density (m ²) (SE)	Range	No. sites (%)	Mean density (m ²) (SE)	Range
Upland bully	31 (82)	0.87 (0.12)	0.03 – 2.1	10 (91)	0.59 (0.17)	0.06 – 1.4
Brown trout	13 (34)	0.62 (0.34)	0.03 – 4.6	7 (64)	0.03 (0.01)	0.01 – 0.1
Longfinned eel	1 (3)	0.05	-	4 (36)	0.04 (0.006)	0.03 – 0.05
Torrentfish	1 (3)	0.06	-	1 (9)	0.08	-
Canterbury galaxias	0	-	-	5 (45)	0.26 (0.09)	0.01 – 0.51
Common bully	0	-	-	1 (9)	0.21	-
Bluegill bully	0	-	-	1 (9)	0.007	-

Mean species richness was significantly greater in the natural streams than in the water races (*t*-test, $P < 0.0001$) and no difference in density was found between the water races and natural streams (Fig. 2). Species richness in the water races was positively correlated with water depth, current velocity and substrate size, and was negatively correlated with Pfankuch index score (Table 3). However, fish density and the abundances of the common species in the water races were not correlated with any physical or chemical variable measured in this study (Table 3). In the natural streams, Canterbury galaxias density was positively correlated with current velocity, and longfinned eel density negatively associated with water depth (Table 3). There were no correlations between the densities of any species with each other in either water races or natural streams (Table 4).

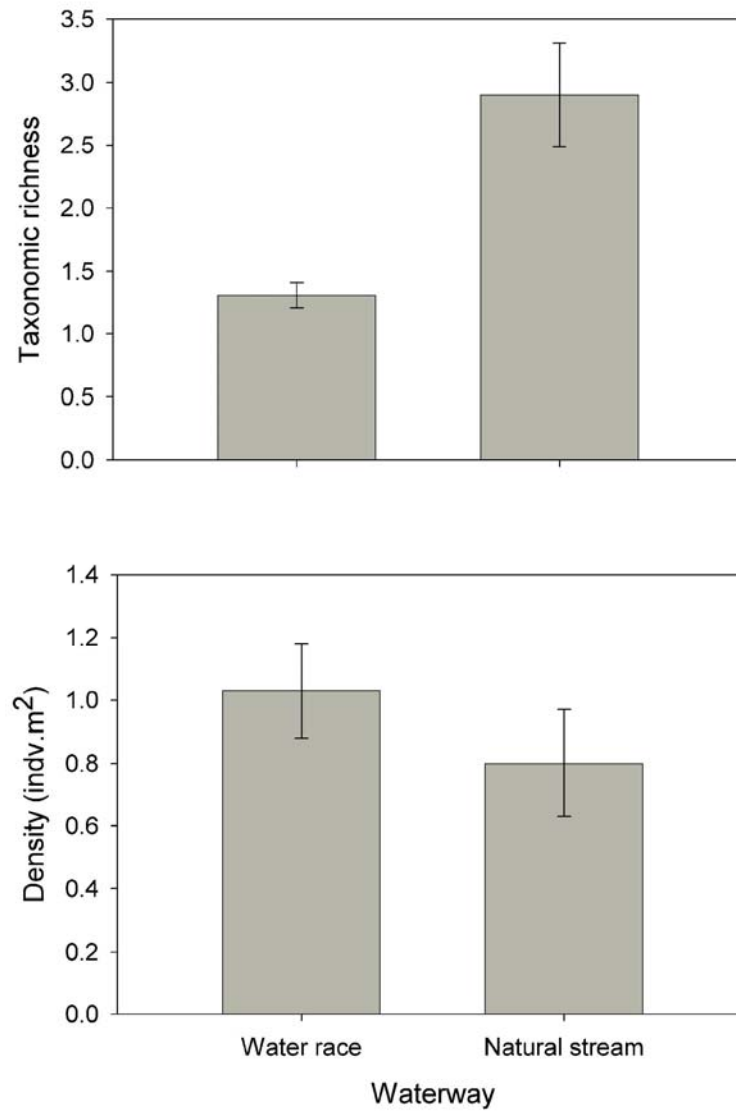


Figure 2. Fish taxonomic richness and density (individuals per m²) in water races and natural streams.

Table 3. Pearson correlation coefficients for richness, total density and densities of individual species with physical and chemical parameters in water races and natural streams. Substrate het = substrate heterogeneity, Temp = temperature, Cond = conductivity. Values in bold font are significant. Significance codes: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Width	Depth	Velocity	Substrate size	Substrate het	Pfankuch	Temp	Cond	DO	Turbidity
Water race										
Richness	0.26	0.37*	0.56**	0.33*	0.00	-0.54**	-0.15	0.17	0.10	-0.08
Total density	-0.20	0.09	0.02	0.16	0.08	0.02	0.09	-0.08	-0.15	0.09
<i>Species density</i>										
Upland bully	-0.19	0.32	-0.05	-0.04	0.16	0.07	-0.13	-0.11	0.04	0.33
Brown trout	-0.07	-0.18	0.06	0.01	-0.04	-0.03	0.24	0.00	-0.21	-0.20
Natural stream										
Richness	0.42	-0.56	-0.19	-0.14	-0.03	0.13	0.62	0.07	-0.49	-0.29
Total density	0.40	-0.04	0.42	0.21	0.31	-0.24	-0.34	0.42	0.42	-0.35
<i>Species density</i>										
Upland bully	0.33	-0.17	0.19	0.08	0.26	-0.06	-0.32	0.56	0.35	-0.18
Brown trout	-0.01	-0.14	-0.19	0.15	0.09	-0.10	0.36	-0.48	-0.51	0.13
Canterbury galaxias	0.17	0.51	0.84**	0.38	0.17	-0.60	-0.34	-0.30	0.45	-0.46
Longfinned eel	0.36	-0.65*	-0.45	-0.17	0.00	0.42	0.33	0.56	-0.26	-0.12

Table 4. Pearson correlation coefficients for each individual species with other species for water races and natural streams. Values in bold font are significant. Significance codes: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Brown trout	Upland bully	Longfinned eel
Water race			
Upland bully	-0.24		
Natural stream			
Upland bully	0.10		
Longfinned eel	-0.23	0.36	
Canterbury galaxias	-0.21	0.04	-0.42

Discussion

Stock water races on the Canterbury Plains had a very depauperate fish community; only two species were commonly found throughout the race network (upland bully and brown trout). The species richness of the natural streams in this study was similar to the national average of three species per site reported by Jowett and Richardson (1996a) from the New Zealand Freshwater Fish Database (NZFFD; McDowall & Richardson, 1983), but lower than the average of five per site recorded in their own New Zealand-wide study. An examination of NZFFD records suggests a species

richness of three to five is common for streams and rivers on the Canterbury Plains. Although the species richness of natural streams in this study was not markedly higher than that of the water races, the natural streams contained representatives of a greater number of fish species that are typical of streams and rivers on the Canterbury Plains (McDowall, 2000). However, the natural streams did lack fish species that are typically excluded from agricultural catchments, such as *Galaxias brevipinnis* and *G. fasciatus* (Jowett & Richardson, 2003; McDowall, 1990). Landuse has been shown to be a major factor influencing the distribution of native fish in New Zealand's streams and rivers, while in-stream habitat conditions, diadromy and the presence of introduced brown trout are also important factors (Hayes et al., 1989; Minns, 1990; Jowett & Richardson, 1995; McDowall, 2000). These four conditions all apply to stock water races and may explain the occurrence, and more importantly the absence of native fish species in the water race sites in this study.

The water races provided a highly modified and homogeneous in-stream habitat, with uniform, shallow, narrow channels and low discharge. They had no pools, only riffles and runs, and had a homogeneous substrate dominated by small pebbles. Water races also generally lacked woody debris, and overhanging banks and vegetation that many fish species prefer for cover (McDowall, 1990). In contrast, the natural streams had heterogeneous channel beds, riffle-run-pool complexes and a diversity of substrate sizes. Most of the natural streams also had overhanging vegetation or banks. These differences in habitat almost certainly influenced the occurrence of fish species, with the homogeneous and low-cover habitat in water races probably severely limiting the species that can survive in the race system. Native galaxiids, which are generally benthic, require cobble substrates to provide shelter from predators and an area for foraging and nesting (McDowall, 1990; Jowett & Richardson, 1995). Even upland bullies, which were common in the water races, have been found to prefer experimental reaches containing greater numbers of cobbles, with most individuals found to dwell under the cobbles (Jowett & Boustead, 2001).

Interestingly, water races supported similar densities of fish to the natural streams. This was primarily due to considerable numbers of upland bullies occurring in many water races. Upland bullies are widespread in the South Island, and are commonly found in a range of rivers from coastal to inland areas (McDowall, 2000). It was the

commonest species in both the water races and the natural streams in this study. Upland bullies tolerate a wide range of habitats, from stony bedded rivers to small, sandy and weedy streams (McDowall, 1990). Because they tend to dwell in the shallow, slow-flowing margins of streams (Jowett & Richardson, 1995), they appear to be well suited to water races. I found upland bullies in all types of water races, including some of the smallest and shallowest. Minns (1990) interrogated patterns of association of New Zealand freshwater fish from entries recorded in the NZFFD and found that upland bully was a notable exception to the usual native-exotic species segregation, being strongly linked with brown trout. I found no negative effect of brown trout abundance on upland bully abundance in either the water races or the natural streams in this study. The benthic feeding habit of upland bully probably allows it to co-exist with brown trout, which are drift-feeders (Cadwallader, 1975a, 1975c), and its preference for stream margins and slower waters (Jowett & Richardson, 1995) probably helps it to avoid trout predation.

Brown trout was the other common species in stock water races. They are usually associated with deep pools or overhanging banks and cooler waters (McDowall, 1990), which are not a feature of water races. However, a large-scale study of brown trout distributions in New Zealand rivers found high brown trout abundance was associated with low gradients and stable flows (Jowett, 1990). The stable hydrology of water races may therefore enhance their habitat suitability to brown trout, regardless of the availability of cover, and the high summer water temperatures.

Although only one longfinned eel was found among the water race sites, they were probably more common in water races than was apparent in this study; five longfinned eels were found among 11 sites in a longitudinal study of stock water races (Chapter 2). The longitudinal study suggested eels were only found in the deeper water races, and as many of the water races sampled in this study were small, they may not generally provide suitable permanent eel habitat. The single torrentfish found in the water races was likely to have been an anomaly. Torrentfish are sea migratory and would have difficulty completing their lifecycle using the stock water races because very few water races flow to the sea.

Many of New Zealand's other native fish are diadromous, including several galaxiid and bully species (McDowall, 1990), and it is likely that populations of these fish species will also be excluded from the stock water race system. However, the non-diadromous Canterbury galaxiid is common in streams and rivers throughout the Canterbury region (McDowall, 2000), and was found in a number of the natural streams in this study. Canterbury galaxias could enter the stock water race network through the water intakes, as the other species presumably have, but because they were absent from the water races in this study, their survival must be very low in these systems. The habitat found in water races may not be suitable for Canterbury galaxias, as they are benthic, and prefer to live, feed and lay their eggs among cobble substrates (McDowall, 1990; Jowett & Richardson, 1995). In addition, the homogeneity of current, particularly the lack of pools and backwaters, might limit the survival of populations; the survival of their fry has been found to be influenced by the extent of backwater habitat (Jellyman & McIntosh, 2008).

In addition, galaxiid distributions have been shown to be restricted by the presence of brown trout (Townsend & Crowl, 1991; Crowl et al., 1992; Townsend, 1996; McDowall, 2006). Trout predate upon both fry (Jellyman & McIntosh, 2008) and adult galaxiids (McIntosh, 2000), and the diets and habitats of many galaxiids, including Canterbury galaxias, overlap with those of brown trout (Cadwallader, 1975b, 1975c; McIntosh et al., 1992). Brown trout is an aggressive competitor that native species are unlikely to out-compete (Townsend, 1996). The small size of the water races, and their homogeneous habitat and lack of cover, might be expected to magnify the effect of trout competition and predation on the native non-diadromous galaxiids, consequently preventing populations from existing in the water race system.

Canterbury mudfish (*Neochanna burrowsius*; Galaxiidae), one of New Zealand's most threatened freshwater fish (Hitchmough et al. 2007), have been found in stock water races in previous studies. There are 10 records of Canterbury mudfish in stock water races in the NZFFD, and a few papers have identified stock water races containing Canterbury mudfish (Eldon et al., 1978; Eldon, 1979; O'Brien and Dunn, 2006). A number of these records are from one area (Hororata township), and are probably part of population originating in the nearby foothills. O'Brien and Dunn

(2006) caught several mudfish at each of three sites in the Hororata township, but as most fish were small they suggested the population was not permanent, but contained juvenile fish sourced from nearby habitat. However, they also suggested that the presence of two large females indicated a reproducing population could exist in the water races. Interestingly, some of the NZFFD records are from very different locations on the Canterbury Plains, including water races nearer the coast. I did not find Canterbury mudfish in water races in this study, however all previous studies of water races used Gee minnow traps, whereas I used electric fishing, which may not be an effective way of catching mudfish. However, it is more likely that the fast-flowing habitats sampled in my water races were not suitable for Canterbury mudfish, as they prefer slow-flowing, spring and wetland habitats (Eldon, 1979). Also, predation by brown trout and eels would prevent existence of Canterbury mudfish in many water races (O'Brien, 2005).

Conclusion

The fish community of the stock water race system was very depauperate, with only one native and one introduced species commonly occurring. Although the densities of fish in water races and natural streams were similar, race communities tended to be a monoculture, usually of upland bully. The stock water race system is probably the most abundant permanent freshwater ecosystem on the Canterbury Plains, and a study of its benthic macroinvertebrate communities suggested it could be an important source of biodiversity in the region, and a refuge for many stream macroinvertebrate taxa (Chapter 1). However, aside from upland bully, stock water races do not provide a refuge for native fish species that are threatened by the habitat loss caused by the summer drying of natural streams. Because stock water races do not provide a migratory pathway to the sea, they could not support populations of native diadromous galaxiid and bully species. Poor habitat suitability to most native fish species combined with presence of introduced brown trout also prevents non-diadromous galaxiid populations from existing in water races. However, an increase in habitat quality, including addition larger substrates and pool or backwater habitats, could make water races a suitable habitat for Canterbury galaxias.

Conclusion

Numerous studies have focused on the large braided rivers and smaller natural streams of the Canterbury Plains (Sagar, 1986; Scrimgeour et al., 1988; Wright-Stow, 2001; Rickard, 2005; Datry et al., 2007). By contrast, the ecology of the stock water race network is relatively poorly known, and yet these race networks provide a significant source of surface water habitat on the plains. However, the habitat of the water races is highly modified and homogeneous. In this thesis, I have shown that, compared to natural streams, water race channels are narrow, shallow and have small, homogeneous substrate. The quality of the habitat in water races is further limited by the agricultural activities of the landscape that surrounds them, and the annual dredging of some water races will also influence habitat. Nevertheless, unlike many natural streams on the plains, the water races are permanently flowing and therefore provide a very stable habitat. These characteristics of the water race habitat have strongly influenced the invertebrate and fish communities, and have made the water race communities distinct to those of Canterbury's natural streams (Fig. 1).

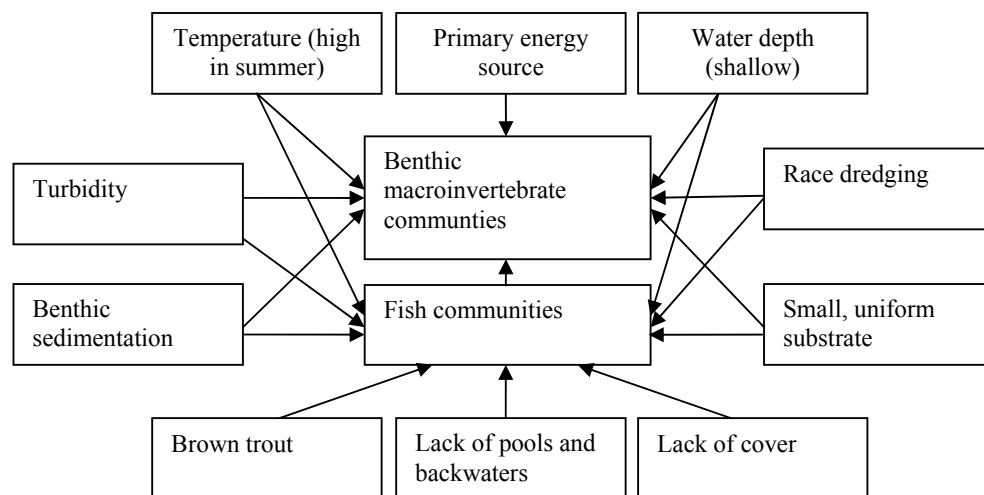


Figure 1. Important factors influencing benthic macroinvertebrate and fish communities in stock water races.

The macroinvertebrate and fish communities of water races

Water races contained a range of benthic macroinvertebrate taxa. However, communities throughout the race network tended to be less diverse than natural streams and were dominated by taxa with generalist habitat requirements, particularly the beetle, *Hydora*, *Deleatidium* mayflies and the snail, *Potamopyrgus*. This was in contrast to the natural streams in this study, which had greater variability of habitats and supported higher diversities and a variety of benthic macroinvertebrate community assemblages. Despite these differences in the assemblage compositions of water races and natural streams, many taxa common to natural streams were also found in water races. For these taxa, the water races provide an important refuge during dry periods in natural streams, and flying adult insects from water races are a potential source of colonists for natural streams when flow returns. Furthermore, water races may increase overall biodiversity in the region as they contained a number of taxa that were not also present in the natural streams.

Water races did not support a great diversity of fish species, but although only two species were common in races (upland bully [*Gobiomorphus breviceps*] and brown trout [*Salmo trutta*]), fish density was similar between water races and natural streams. Upland bullies appeared to be well suited to the water race habitat, probably because they naturally prefer to dwell in shallow areas of streams (Jowett & Richardson, 1995), and the stable hydrology of water races may create favourable habitat for brown trout. Aside from these two common species, water races do not provide an important habitat for fish species on the Canterbury Plains, nor are they a refuge for the many fish species that are threatened by the habitat loss in natural streams. There are probably several reasons for this. Diadromous life history prevents populations of a number of native fish species from occurring in the water race network, because races rarely flow to the sea. However races also probably provide poor physical habitat conditions for many native fish, particularly lack of pools, backwaters and instream cover. Furthermore, the presence of introduced brown trout probably excludes populations of many non-diadromous species from water races.

Management and future of water races

Williams et al. (2003), with a study from Southern England, provides one of the few other examples of a comparison of the biodiversity in different types of waterbodies in a landscape that included man-made waterways, in this case ditches. These ditches were found to provide a valuable habitat for taxa that were rare in the other waterbody types studied. The authors concluded all waterbody types, including small and man-made waterbodies, contributed to the biodiversity of a landscape, and therefore were valuable habitats to include in regional biodiversity plans.

There has been ongoing debate about closing stock water races (e.g., RF, 2006) for various reasons, including easing pressure on source rivers, freeing up allocation for other users, inefficiency, and poor water quality (Morgan et al., 2002). However, my research has shown that stock water races provide an important source of aquatic biodiversity on the plains, both alongside natural streams and own their own. However, despite an inconclusive result in the substrate manipulation experiment, the research in this thesis indicates that the benthic macroinvertebrate and fish communities of the water races are limited by the highly homogenous habitat of the race channels.

Improving the ecology of water races

The biodiversity value of stock water races could be improved with enhancement of instream habitat. Although habitat manipulation would be restricted by the requirement to preserve the functionality of water races, some of the larger races that require minimal maintenance (i.e. dredging) could be suitable for habitat improvement. An increase in the range of substrate sizes could increase habitat for invertebrates and fish, particularly native galaxiids (McDowall, 2000) and establishment of variation in current velocity, especially pools and backwaters, could also increase galaxiid habitat. Riparian vegetation could stabilise banks, thereby reducing sedimentation and increase shade that would reduce high summer water temperatures and control excess macrophyte and algal growth (Quinn, 2000), and these modifications could also reduce the need for race dredging.

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References

Australian Bureau of Agricultural and Resource Economics & New Zealand Ministry of Agriculture and Forestry 2006. Agriculture economies of Australia and New Zealand: past, present, future. ABARE, Canberra.

Allan, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology*, 56(5): 1040-1053.

Allan, J. D. & Castillo, M. M. 2007. Stream ecology: structure and functioning of running waters (2nd edition). Springer, Dordrecht, The Netherlands.

Allan, J. D. & Flecker, A. S. 1993. Biodiversity conservation in running waters. *BioScience*, 43(1): 32-43.

American Public Health Association, 2005. Standard Methods for the Examination of Water and Wastewater, 21st Edition. APHA, AWWA and WEF, Washington DC.

Armitage, P. D. 2006. Long-term faunal changes in a regulated and an unregulated stream – Cow Green thirty years on. *River Research and Applications*, 22(9): 947-966.

Baptista, D. F., Dorvillé, L. F. M., Buss, D. F. & Nessiamian, J. L. 2001. Spatial and temporal organization of aquatic insect assemblages in the longitudinal gradient of a tropical river. *Revista Brasileira de Biologia*, 61(2): 295-304.

Barmuta, L. A. & Lake, P. S. 1982. On the value of the River Continuum Concept. *New Zealand Journal of Marine and Freshwater Research*, 16: 227-229.

Beisel, J. N., Usseglio-Polatera, P., Thomas, S. & Moreteau, J. C. 1998. Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. *Hydrobiologia*, 389(1-3): 73-88.

- Beisel, J. N., Usseglio-Polatera, P. & Moreteau, J. C. 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia*, 422/423: 163-171.
- Bernhardt, E. S., Palmer, M. A., Allan, J. D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-Shah, J., Galat, D., Gloss, S., Goodwin, P., Hart, D., Hassett, B., Jenkinson, R., Katx, S., Kondof, G. M., Lake, P. S., Lave, R., Meyer, J. L., O'Donnell, T. K. O., Pagano, L., Powell, B. & Sudduth, E. 2005. Synthesizing U.S. river restoration efforts. *Science*, 308(5722): 636-637.
- Biggs, B. J. F. 1996. Patterns in benthic algae of streams. *In*: Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego. Pp. 31-56.
- Bond, N. R. & Lake, P. S. 2003. Local habitat restoration in streams: Constraints on the effectiveness of restoration for stream biota. *Ecological Management & Restoration*, 4(3): 193-198.
- Boothroyd, I. & Stark, J. 2000. Use of invertebrates in monitoring. *In*: Collier, K. J. & Winterbourn, M. J. *eds*. *New Zealand stream invertebrates: ecology and implications for management*. New Zealand Limnological Society, Christchurch. Pp 344-373.
- Boyero, L. 2003. The quantification of local substrate heterogeneity in streams and its significance for macroinvertebrate assemblages. *Hydrobiologia*, 499(1-3):161-168.
- Brasher, A. M. D. 2003. Impacts of human disturbances on biotic communities in Hawaiian streams. *BioScience* 53(11): 1052-1060.
- Briers, R. A., Cariss, H. M. & Gee, J. H. R. 2002. Dispersal of adult stoneflies (Plecoptera) from upland streams draining catchments with contrasting land-use. *Archiv für Hydrobiologie*, 155(4): 627-644.
- Brittain, J. E. & Eikeland, T. J. 1988. Invertebrate drift – A review. *Hydrobiologia*, 166(1): 77-93.

- Brooks, A. J., Haeusler, T., Reinfelds, I. & Williams, S. 2005. Hydraulic microhabitats and the distribution of macroinvertebrate assemblages in riffles. *Freshwater Biology*, 50(2): 331-344.
- Cadwallader, P. L. 1975a. Feeding habits of two fish species in relation to invertebrate drift in a New Zealand river. *New Zealand Journal of Marine and Freshwater Research*, 9(1): 11-26.
- Cadwallader, P. L. 1975b. The food of the New Zealand common river galaxias, *Galaxias vulgaris* Stokell (Pisces: Salmoniformes). *Australian Journal of Marine and Freshwater Research*, 26(1): 15-30.
- Cadwallader, P. L. 1975c. Feeding relationships of galaxiids, bullies, eels and trout in a New Zealand river. *Australian Journal of Marine and Freshwater Research*, 26(3): 299-316.
- Canton, S. P. & Chadwick, J. W. 1983. Seasonal and longitudinal changes in invertebrate functional groups in the Dolores River, Colorado, 2(1): 41-47.
- Church, M. 2002. Geomorphic thresholds in riverine landscapes. *Freshwater Biology*, 47(4): 541-557.
- Cockayne, L. 1927. Ecological botany of the Canterbury Plains. *In: Natural history of Canterbury eds Speight, R., Wall, A. & Laing, R. M. Simpson and Williams Ltd.*, Christchurch, New Zealand
- Collier, K. J. & Smith, B. J. 1997. Dispersal of adult caddisflies (Trichoptera) into forests alongside three New Zealand streams. *Hydrobiologia*, 361(1-3): 53-65.
- Colwell, R. K. 2006. *EstimateS*: Statistical estimation of species richness and shared species from samples. Version 8. Persistent URL <purl.oclc.org/estimates>.
- Cowie, B. 1985. An analysis of changes in the invertebrate community along a southern New Zealand montane stream. *Hydrobiologia*, 120(1): 35-46

- Crowl, T. A., Townsend, C. R. & McIntosh, A. R. 1992. The impact of introduced brown and rainbow trout on native fish: the case of Australasia. *Reviews in Fish Biology and Fisheries*, 2(3): 217-241.
- Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *American Midland Naturalist*, 67(2): 477-504.
- Cummins, K. W. 1974. Structure and function of stream ecosystems. *BioScience*, 24(11): 631-641.
- Cummins, K. W. and Lauff, G. H. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia*, 34(2): 145-181.
- Cushing, C. E., McIntire, C. D., Cummins, K. W., Minshall, G. W., Petersen, R. C., Sedell, J. R. & Vannote, R. L. 1983. Relationships among chemical, physical and biological indices along a river continua based on multivariate analysis. *Archiv für Hydrobiologie*, 98(3): 317-326.
- Cushing, C. E., Cummins, K. W. & Minshall, G. W. 1995. *River and stream ecosystems*. Elsevier, New York.
- Datry, T., Larned, S. T. & Scarsbrook, M. R. 2007. Responses of hyporheic invertebrate assemblages to large-scale variation in flow permanence and surface-subsurface exchange. *Freshwater Biology* 52(8): 1452-1462.
- Davidson, J. 1987. *The prehistory of New Zealand*. Longman Paul, Auckland, New Zealand.
- Davies-Colley, R. J. 1997. Stream channels are narrower in pasture than in forest. *New Zealand Journal of Marine and Freshwater Research*, 31(5): 599-608.
- de Lisle, J. F. 1969. The climate and weather. *In*: Knox, G. A. *ed.* *The natural history of Canterbury*. A. H. and A. W. Reed, Wellington, New Zealand. Pp 68-76.

- Delong, M. D. & Brusven, M. A. 1994. Allochthonous input of organic matter from different riparian habitats of an agriculturally impacted stream. *Environmental Management*, 18(1): 59-71.
- Delong, M. D. & Brusven, M. A. 1998. Macroinvertebrate community structure along the longitudinal gradient of an agriculturally impacted stream. *Environmental management*, 22(3): 445-457.
- Doisy, K. E. & Rabeni, C. F. 2001. Flow conditions, benthic food resources, and invertebrate community composition in a low-gradient stream in Missouri. *Journal of the North American Benthological Society*, 20(1): 17-32.
- Downes, B. J., Lake, P. S., Schreiber, E. S. G. & Glaister, A. 1998. Habitat structure and regulation of local species diversity in a stony, upland stream. *Ecological Monographs*, 68(2): 237-257.
- Downes, B. J., Lake, P. S., Schreiber, E. S. G. & Glaister, A. 2000. Habitat structure, resources and diversity: the separate effects of surface roughness and macroalgae on stream invertebrates. *Oecologia*, 123(4): 569-581.
- Douglas, M. & Lake, P. S. 1994. Species richness of stream stones: an investigation of the mechanisms generating the species-area relationship. *Oikos*, 69(1): 387-396.
- Dudley, T. L., Cooper, S. D. & Hemphill, N. 1986. Effects of macroalgae on a stream invertebrate community. *Journal of the North American Benthological Society*, 5(2): 93-106.
- Eddington, J. M. 1968. Habitat preferences in net-spinning caddis larvae with special reference to the influence of water velocity. *The Journal of Animal Ecology*, 37(3): 675-692.
- Eldon, G. A. 1979. Habitat and interspecific relationships of the Canterbury mudfish, *Neochanna burrowsius* (Salmoniformes: Galaxiidae). *New Zealand Journal of Marine and Freshwater Research*, 13(1): 111-119.

Eldon, G. A., Howden, P. J. & Howden, D. B. 1978. Reduction of a population of Canterbury mudfish, *Neochanna burrowsius* (Galaxiidae), by drought. New Zealand Journal of Marine and Freshwater Research, 12(4): 313-321.

Fitzharris, B. B., Mansergh, G. D. & Soons, J. M. 1992. Basins and lowlands of the South Island. *In*: Soons, J. M. & Selby, M. J. Landforms of New Zealand. Longman Paul, Hong Kong. Pp 407-423.

Flecker, A. S. & Allan, J. D. 1984. The importance of predation, substrate and spatial refugia in determining lotic insect distributions. *Oecologia*, 64(3): 306-313.

Foley, J. A., DeFries, R., Anser, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., Snyder, P. K. 2005. Global consequences of land use. *Science*, 309(5734): 570-574.

Gage, M. 1969. Rocks and landscape . *In*: Knox, G. A. *ed*. The natural history of Canterbury. A. H. and A. W. Reed, Wellington, New Zealand. Pp 25-43.

Georgian, T. & Thorp, J. H. 1992. Effects of microhabitat selection on feeding rates of net-spinning caddisfly larvae. *Ecology*, 73(1): 229-240.

Giller, P. & Malmqvist, B. 1998. The biology of streams and rivers. Oxford University Press.

Gotelli, N. J. & Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4(4):379-391.

Graham, A. A. 1990. Siltation of stone-surface periphyton in rivers by clay-sized particles from low concentration in suspension. *Hydrobiologia*, 199(2): 107-115.

- Gray, D., Scarsbrook, M. R. & Harding, J. S. 2006. Spatial biodiversity patterns in a large New Zealand braided river. *New Zealand Journal of Marine and Freshwater Research*, 40(4): 631-642.
- Greathouse, E. A. & Pringle, C. M. 2006. Does the river continuum concept apply on a tropical island? Longitudinal variation in a Puerto Rican stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(1): 134-152.
- Grubaugh, J. W., Wallace, J. B. & Houston, E. S. 1996. Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(4): 896-909.
- Hanchet, S. M. 1990. Effect of land use on the distribution and abundance of native fish in tributaries of the Waikato River in the Hakarimata Range, North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 24: 159-171.
- Harding, J. S. 1992. Discontinuities in the distribution of invertebrates in impounded South Island rivers, New Zealand. *Regulated Rivers: Research & Management*, 7(4): 327-335.
- Harding, J. S. 1994. Lotic Ecoregions of New Zealand. Unpublished Ph.D. thesis, University of Canterbury.
- Harding, J. S. & Winterbourn, M. J. 1995. Effects of contrasting land use on physico-chemical conditions and benthic assemblages of streams in a Canterbury (South Island, New Zealand) river system. *New Zealand Journal of Marine and Freshwater Research*, 29(4): 479-492.
- Harding, J. S., Young, R. G., Hayes, J. W., Shearer, K. A. & Stark, J. D. 1999. Changes in agricultural intensity and river health along a river continuum. *Freshwater Biology*, 42(2): 345-357.

Hart, D. D. 1978. Diversity in Stream Insects: Regulation by Rock Size and Microspatial Complexity. Proceedings: 20th Congress, Internationale Vereinigung für Theoretische und Angewandte Limnologie; Copenhagen, Denmark 8 August 1977. Vol. 20, part 2, p 1376-1381.

Hart, D. D. & Finelli, C. M. 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics*, 30: 363-395.

Hawkins, C. P. & Sedell, J. R. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon Streams. *Ecology*, 62(2): 387-397.

Hayes, J. W., Leathwick, J. R. & Hanchet, S. M. 1989. Fish distribution patterns and their association with environmental factors in the Mokau River catchment, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 23: 171-180.

Hitchmough, R., Bull, L. & Cromarty, P. 2007. New Zealand threat classification system lists 2005. Science and Technical Publishing Report, Department of Conservation, Wellington, New Zealand.

Hynes, N. B. H 1970. *The Ecology of Running Waters*. Liverpool University Press, UK.

Jellyman, P. G. & McIntosh, A. R. 2008. The influence of habitat availability and adult density on non-diadromous galaxiid fry settlement in New Zealand. *Journal of Fish Biology*, 72(1): 143-156.

Jones, E. B. D., Helfman, G. S., Harper, J. O. & Bolstad, P. V. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. *Conservation Biology*, 13(6): 1454-1465.

Jowett, I. G. 1990. Factors related to the distribution and abundance of brown and rainbow trout in New Zealand clear-water rivers. *New Zealand Journal of Marine and Freshwater Research*, 24: 429-440.

Jowett, I. G. 2000. Flow management. *In*: Collier, K. J. & Winterbourn, M. J. *eds.* New Zealand stream invertebrates: ecology and implications for management. New Zealand Limnological Society, Christchurch. Pp. 289-312.

Jowett, I. G. 2003. Hydraulic constraints on habitat suitability for benthic invertebrates in gravel-bed rivers. *River Research and Applications*, 19(5-6): 495-507.

Jowett, I. G. & Boustead, N. C. 2001. Effects of substrate and sedimentation on the abundance of upland bullies (*Gobiomorphus breviceps*). *New Zealand Journal of Marine and Freshwater Research*, 35(3): 605-613.

Jowett, I. G. & Richardson, J. 1990. Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of in-stream flow-habitat models from *Deleatidium* spp. *New Zealand Journal of Marine and Freshwater Research*, 24: 19-30.

Jowett, I. G. & Richardson, J. 1995. Habitat preferences of common, riverine New Zealand native fishes and implications for flow management. *New Zealand Journal of Marine and Freshwater Research*, 29(1): 13-23.

Jowett, I. G. & Richardson, J. 2003. Fish communities in New Zealand rivers and their relationship to environmental variables. *New Zealand Journal of Marine and Freshwater Research*, 37(2): 347-366.

Jowett, I. G., Richardson, J., Biggs, B. J. F., Hickey, C. W. & Quinn, J. M. 1991. Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, 25: 187-199.

- Karr, J. R., Toth, L. A. & Dudley, D. R. 1985. Fish communities of midwestern rivers: A history of degradation. *BioScience*, 35(2): 90-95.
- Kovats, Z., Ciborowski, J. & Corkum, L. 1996. Inland dispersal of adult aquatic insects. *Freshwater Biology*, 36(2): 265-276.
- Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19(4): 573-592.
- Larned, S. T., Hicks, D. M., Schmidt, J., Davey, A. J. H., Dey, K., Scarsbrook, M., Arscott, D. B. & Woods, R. A. 2008 The Selwyn River of New Zealand: a benchmark system for alluvial plain rivers. *River Research and Applications*, 24(1): 1-21.
- Larson, M. G., Booth, D. B. & Morley, S. A. 2001. Effectiveness of large woody debris in stream rehabilitation projects in urban basins. *Ecological Engineering* 18(2): 211-226
- Lemly, A. D., Kingsford, R. T. & Thompson, J. R. 2000. Irrigated agriculture and wildlife conservation: conflict on a global scale. *Environmental Management*, 25(5): 485-512.
- Morgan, M., Bidwell, V., Bright, J., McIndoe, I. & Robb, C. 2002. Canterbury strategic water study. Lincoln Environmental report no 4557/1.
- Logan, R. 1987. Waimakariri: Canterbury's "river of cold rushing water". Logan Print, Gisborne, New Zealand.
- Maitland, P. S. 1995. The conservation of freshwater fish: past and present experience. *Biological Conservation*, 72(2): 259-270.
- Matson, P. A., Parton, W. J., Power, A. G. & Swift, M. J. 1997. Agricultural intensification and ecosystem properties. *Science*, 277(5325): 504-509.

- Matthaei, C. D., Weller, F., Kelly, D. W. & Townsend, C. R. 2006. Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology*, 51(11): 2154-2172.
- May, R. M. 1975. Patterns of species abundance and diversity. *In*: Cody, M. L. and Diamond, J. M. *eds*. *Ecology and Evolution of Communities*. Belknap Press of Harvard University, Cambridge, Massachusetts, USA. Pp. 81-120
- McCune, B. and Mefford, J. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4.41. MjM Software, Gleneden Beach, Oregon, U.S.A.
- McDowall, R. M. 1990. *New Zealand freshwater fishes; a natural history and guide*. Heinemann Reed, Auckland.
- McDowall, R. M. 2000. *The Reed field guide to New Zealand freshwater fishes*. Reed, Auckland.
- McDowall, R. M. & Richardson, J. 1983. *The New Zealand freshwater fish survey: guide to input and output*. Fisheries Research Division, Information Leaflet 12.
- McGlone, M. S. 1989. The Polynesian settlement of New Zealand in relation to environmental and biotic changes. *New Zealand Journal of Ecology* 12(s): 115-129.
- McIntosh, A. R. 2000. Habitat- and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(10): 2140-2151.
- McIntosh, A. R., Townsend, C. R. & Crowl, T. A. 1992. Competition for space between introduced brown trout (*Salmo trutta* L.) and a native galaxiid (*Galaxias vulgaris* Stokell) in a New Zealand stream. *Journal of Fish Biology* 41(1): 63–81.
- Meredith, A. S. & Hayward, S. A. 2002. An overview of the water quality of the rivers and streams of the Canterbury region. Environment Canterbury report no. R02/25.

- Meredith, A. S., Cottam, D., Anothony, M. & Lavender, R. 2003. Ecosystem health of Canterbury rivers: development and implementation of biotic and habitat assessment methods 1999/2000. Environment Canterbury report no. R03/3.
- Mérigoux, S. & Dolédec, S. 2004. Hydraulic requirements of stream communities: a case study on invertebrates. *Freshwater Biology*, 49(5): 600-613.
- Minns, C. K. 1990. Patterns of distribution and association of freshwater fish in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 24: 31-44.
- Minshall, G. W. 1984. Aquatic insect-substratum relationships. *In*: Resh, V. H. & Rosenberg, D. M. *eds*. The ecology of aquatic insects, New York. Praeger Publishers, pp. 358-400.
- Minshall, W., Peterson, R. C., Cummins, K. W., Bott, T. L., Sedell, J. R., Cushing, C. E. & Vannote, R. L. 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs*, 53(1): 2-25.
- Graynoth, E. 1979. Effects of logging on stream environments and faunas in Nelson. *New Zealand Journal of Marine and Freshwater Research*, 13(1): 79-109.
- Morgan, D. R. & Graynoth, E. 1978. The influence of forestry practices on the ecology of freshwater fish in New Zealand. New Zealand Ministry of Agriculture & Fisheries, Fisheries Research Occasional Publication 14.
- Morgan, M., Bidwell, V., Bright, J., McIndoe, I. & Robb, C. 2002. Canterbury strategic water study. Lincoln Environmental report no 4557/1.
- Naiman, R. J. & Turner, M. G. 2000. A future perspective on North America's freshwater ecosystems. *Ecological Applications*, 10(4): 958-970.
- Negishi, J.N., Inoue, M. & Nunokawa, M. 2002. Effects of channelisation on stream habitat in relation to a spate and flow refugia for macroinvertebrates in northern Japan. *Freshwater Biology*, 47(8): 1515-1529.

Nevens, T. H. F. 1965. River classification with particular reference to New Zealand. Proceedings, 4th New Zealand Geography Conference, Dunedin, 83-90.

O'Brien, L. K. 2005. The conservation ecology of Canterbury mudfish (*Neochanna burrowsius*). Unpublished PhD thesis, University of Canterbury, Christchurch, New Zealand.

O'Brien, L. & Dunn, N. 2006. Canterbury mudfish within Hororata Township. Ichthy-niche ecological assessment report.

Ogbeibu, A. E. & Oribhabor, B. J. 2002. Ecological impact of river impoundment using benthic macro-invertebrates as indicators. Water Research, 36(10): 2427-2436.

Palmer, M. A., Ambrose, R. F. & Poff, N. L. 1997. Ecological theory and community restoration ecology. Restoration Ecology, 5(4): 291-300.

Parkyn, S. M., Davies-Colley, R. J., Halliday, N. J., Costley, K. J. & Croker, G. F. 2003. Planted riparian buffer zones in New Zealand: do they live up to expectations? Restoration Ecology, 11(4): 436-447.

Paul, M. J. & Meyer, J. L. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics, 32: 333-365.

Petersen, I., Winterbottom, J. H., Orton, S., Friberg, N., Hildrew, A. G., Spiers, D. C. & Gurney, W. S. C. 1999. Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. Freshwater Biology, 42(3): 401-416.

Petersen, I., Masters, Z., Hildrew, A. G. & Ormerod, S. J. 2004. Dispersal of adult aquatic insects in catchments of differing land use. Journal of Applied Ecology, 41(5): 934-950.

Pfankuch, D. J. 1975. Stream reach inventory and channel stability evaluation. USDA Forest Service Northern Region, Montana.

- Pimentel, D., Houser, J., Preiss, E., White, O., Fang, H., Mesnick, L., Barsky, T., Tariche, S., Schreck, J. & Alpert, S. 1997. Water resources: agriculture, the environment, and society. *BioScience*, 47(2): 97-106.
- Postel, S. L. 2000. Entering an era of water scarcity: the challenges ahead. *Ecological Applications*, 10(4): 941-948.
- Quinn, J. M. 2000. Effects of pastoral development. *In*: Collier, K. J. & Winterbourn, M. J. *eds*. New Zealand stream invertebrates: ecology and implications for management. New Zealand Limnological Society, Christchurch. Pp 208-229.
- Quinn, J. M. & Hickey, C. W. 1990a. Characterisation and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. *New Zealand Journal of Marine and Freshwater Research* 24: 387-409.
- Quinn, J. M. & Hickey, C. W. 1990b. Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 24: 411-427.
- Quinn, J. M. & Stroud, M. J. 2002. Water quality and sediment and nutrient export from New Zealand hill-land catchments of contrasting land use. *New Zealand Journal of Marine and Freshwater Research*, 36(2): 409-429.
- Quinn, J. M., Williamson, R. B., Smith, K. R. & Vickers, M. L. 1992. Effects of riparian grazing and channelisation on streams in Southland, New Zealand. 2. Benthic invertebrates. *New Zealand Journal of Marine and Freshwater Research*, 26: 259-273.
- Quinn, J. M., Steele, G. L., Hickey, C. W. & Vickers, M. L. 1994. Upper thermal tolerances of twelve New Zealand stream invertebrate species. *New Zealand Journal of Marine and Freshwater Research*, 28(4): 391-397.

Quinn, J. M., Cooper, A. B., Davies-Colley, R. J., Rutherford, J. C. & Williamson, R. B. 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. *New Zealand Journal of Marine and Freshwater Research*, 31(5): 579-597.

Rapport, D. J. & Whitford, W. G. 1999. How ecosystems respond to stress. *BioScience*, 49(3): 193-203.

Research First 2006. Results from the 2006 Ellesmere water race survey. Report prepared for Selwyn District Council.

Rempel, L. L., Richardson, J. S. & Healey, M. C. 2000. Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshwater Biology*, 45: 57-73.

Richter, B. D., Braun, D. P., Mendelson, M. A. & Master, L. L. 1997. Threats to imperilled freshwater fauna. *Conservation Biology*, 11(5): 1081-1093.

Rickard, S. 2005. The effects of land management practices on dairy streams in Canterbury. Unpublished MSc thesis, University of Canterbury, Christchurch, New Zealand.

Riley, A. L. 1998: Restoring streams in cities: a guide for planners, policy makers, and citizens. Island Press, Washington, DC.

Riley, R. H., Townsend, C. R., Niyogi, D. K., Arbuckle, C. A. & Peacock, K. A. 2003. Headwater stream response to grassland agricultural development in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 37(2): 389-403.

Rounick, J. S. & Winterbourn, M. J. 1983. Leaf processing in two contrasting beech forest streams: effects of physical and biotic factors on litter breakdown. *Archiv für Hydrobiologie*, 96(4): 448-474.

- Ryan, P. A. 1991. Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research*, 25: 207-221.
- Ryder, G. I. & Scott, D. 1988. Applicability of the River Continuum Concept to New Zealand streams. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie*, 23(3): 1441-1445.
- Sagar, P. M. 1986. The effects of floods on the invertebrate fauna of a large, unstable braided river. *New Zealand Journal of Marine and Freshwater Research*, 20: 37-46.
- Scarsbrook, M. R. 2000. Life-histories *In*: Collier, K. J. & Winterbourn, M. J. *eds*. *New Zealand stream invertebrates: ecology and implications for management*. New Zealand Limnological Society, Christchurch. Pp 76-99.
- Scarsbrook, M. R. & Townsend, C. R. 1993. Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology*, 29(3): 395-410.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science*, 185(4145): 27-39.
- Scott, D. 1973: Animal indicators of organic pollution. *In*: *Proceedings of the Pollution Research Committee*. DSIR Information Series no. 97: 445-456.
- Scott, D., White, J. W. & Rhodes, D. S. 1994. Invertebrate fauna of three stream in relation to land use in Southland, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 28(3): 277-290.
- Scrimgeour, G. J., Davidson, R. J. & Davidson, J. M. 1988. Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand river. *New Zealand Journal of Marine and Freshwater Research*, 22: 337-344.

Shieh, S. H., Kondratieff, B. C., Ward, J. V. & Rice, D. A. 1999. The relationship of macroinvertebrate assemblages to water chemistry in a polluted Colorado plains stream. *Archiv für Hydrobiologie*, 145(4): 405-432.

Smith, W. & Montgomery, H. 2004. Revolution or evolution? New Zealand agriculture since 1984. *GeoJournal*, 59(2): 107-118.

Soulé, M. E. 1991. Conservation: tactics for a constant crisis. *Science*, 253(5921): 744-750.

Stark, J. D. 1985. A macroinvertebrate community index of water quality for stony streams. Water & Soil Miscellaneous Publication no. 87. Wellington, Ministry of Works and Development.

Stark, J. D. 1993. Performance of the Macroinvertebrate Community Index: effects of sampling method, sample replication, water depth, current velocity, and substratum on index values. *New Zealand Journal of Marine and Freshwater Research* 27: 463-478.

Stark, J. D. 1998. SQMCI: a biotic index for freshwater macroinvertebrate coded-abundance data. *New Zealand Journal of Marine and Freshwater Research*, 32(1): 55-66.

Statzner, B. & Higler, B. 1985. Questions and comments on the River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 42(5): 1038-1044.

Statzner, B. & Higler, B. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology*, 16(1): 127-139.

Statzner, B., Gore, J. A. & Resh, V. H. 1988. Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society*, 7(4): 307-360.

- Steinman, A. D., Lamberti, G. A. and Leavitt, P. R. 2007. Biomass and pigments of benthic algae. *In*: Hauer, F. R. and Lamberti, G. A. *eds*. Methods in stream ecology. Pp. 357 – 379.
- Suren, A. M. 2000. Effects of urbanisation *In*: Collier, K. J. & Winterbourn, M. J. *eds*. New Zealand stream invertebrates: ecology and implications for management. New Zealand Limnological Society, Christchurch. Pp 260-288.
- Suren, A. M. & McMurtrie, S. 2005. Assessing the effectiveness of enhancement activities in urban streams: II. Responses of invertebrate communities. *River Research and Applications*, 21(4): 439-453.
- Suren A. M., Riis, T., Biggs, B. J. F., McMurtrie, S. & Barker, R. 2005. Assessing the effectiveness of enhancement activities in urban streams: habitat responses. *River Research and Applications*, 21(4): 381-401.
- Taylor, R. & Smith, I. 1997. The state of New Zealand's Environment. Ministry for the Environment, Wellington.
- Thompson, R. M. and Townsend, C. R. 2000. New Zealand's stream invertebrate communities: an international perspective. *In*: Collier, K. J. & Winterbourn, M. J. *eds*. New Zealand stream invertebrates: ecology and implications for management. New Zealand Limnological Society, Christchurch. Pp. 53 – 74.
- Thompson, R. M. & Townsend, C. R. 2004. Land-use influence on New Zealand stream communities: effects on species composition, functional organization, and food-web structure. *New Zealand Journal of Marine and Freshwater Research*, 38(4): 595-608.
- Townsend, C. R. 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. *Biological Conservation* 78(1): 13-22
- Townsend, C. R. & Crowl, T. A. 1991. Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout? *Oikos*, 61(3): 347-354.

- Usseglio-Polatera, P. & Beisel, J. N. 2002. Longitudinal changes in macroinvertebrate assemblages in the Meuse River: anthropogenic effects versus natural change. *River Research and Applications*, 18(2): 197-211.
- Walser, C. A. & Bart Jr., H. L. 1999. Influence of agriculture on in-stream habitat and fish community structure in Piedmont watersheds of the Chattahoochee River System. *Ecology of Freshwater Fish*, 8(4): 237-246.
- Walsh, C. J., Waller, K. A., Gehling, J. & Mac Nally, R. 2007. Riverine invertebrate assemblages are degraded more by catchment urbanisation than by riparian deforestation. *Freshwater Biology*, 52(3): 574-587.
- Ward, J. V. & Stanford, J. A. 1982. Thermal response in the evolutionary ecology of aquatic insects. *Annual Review of Entomology*, 27: 97-117.
- Wellnitz, P. A., Poff, N. L., Cosyleón, G. & Steury, B. 2001. Current velocity and spatial scale as determinants of the distribution and abundance of two rheophilic herbivorous insects. *Hydrobiologia*, 16(2): 111-120.
- Wilcock, R. J., Nagels, J. W., Rodda, H. J., O'Conner, M. B., Thorrols, B. S. & Barnett, J. W. 1999. Water quality of a lowland stream in a New Zealand dairy farming catchment. *New Zealand Journal of Marine and Freshwater Research*, 33(4): 683-696.
- Williams, D. D. 1980. Some relationships between stream benthos and substrate heterogeneity. *Limnology and Oceanography*, 25(1): 166-172.
- Williams, D. D. & Hynes, H. B. N. 1976. The recolonization mechanisms of stream benthos. *Oikos*, 27(2): 265-272.
- Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P. & Sear, D. 2005. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation*, 115(2): 329-341.

Williamson, R. B., Smith, K. R. & Quinn, J. M. 1992. Effects of riparian grazing and channelisation on streams in Southland, New Zealand. 1. Channel form and stability. *New Zealand Journal of Marine and Freshwater Research*, 26: 241-258.

Winterbourn, M. J. 1973. A guide to the freshwater Mollusca of New Zealand. *Tuatara* 20: 141-159.

Winterbourn, M. J. 1981. The use of aquatic invertebrates in studies of stream water quality. *Water & Soil Miscellaneous Publication 22*. Wellington, Ministry of Works and Development. Pp 5-16.

Winterbourn, M. J. 1982. The River Continuum Concept – replay to Barmuta and Lake. *New Zealand Journal of Marine and Freshwater Research*, 16: 229-231.

Winterbourn, M. J. 2004. Stream invertebrates. *In*: Harding, J., Mosley, P., Pearson, C. & Sorrell, B. *eds* *Freshwaters of New Zealand*. New Zealand Limnological and Hydrological Societies, Christchurch.

Winterbourn, M. J., Rounick, J. S. & Cowie, B. 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* 15: 321-328

Winterbourn, M. J., Gregson, K. L. D. & Dolphin, C. H. 2006. *Guide to the Aquatic Insects of New Zealand* (4th edition). *Bulletin of the Entomological Society of New Zealand*.

Wood, V. & Brooking, T. 2001. *In*: Cant, G. & Kirkpatrick, R. *eds*. *Rural Canterbury: celebrating its history*. Daphne Brassell Associates and Lincoln University Press, Wellington, New Zealand.

Wright-Stow, A. E. 2001. *Biomonitoring, and the macroinvertebrate faunas of Canterbury streams*. Unpublished MSc thesis, University of Canterbury, Christchurch, New Zealand.

Vannote, R. L. & Sweeney, B. W. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist*, 115(5): 667-695.

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. & Cushing, C. E. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(1): 130-137.

Voelz, N. J. and Ward, J. V. 1990. Macroinvertebrate responses along a complex regulated stream environment. *Regulated rivers: research & management* 5(5): 365-374.

Young, R., Smart, G. & Harding, J. 2004. Impacts of hydro-dams, irrigation schemes and river control works. *In: Harding, J. S., Mosley, P., Pearson, C. & Sorrell, B. eds Freshwaters of New Zealand*. New Zealand Limnological and Hydrological Societies, Christchurch. Pp 37.1-37.16.